THE EVOLUTION OF KINSHIP AND MARRIAGE SYSTEMS

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A thesis submitted for the degree of
Doctor of Philosophy

2009

Declaration

I, Laura Fortunato, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

Abstract

Kinship and marriage systems represent the ways in which humans organize relatedness and reproduction. The work presented in this thesis extends the philosophical, theoretical, and methodological foundations of evolutionary biology to the study of these aspects of human social behaviour.

Firstly, a game-theoretic analysis shows that the evolution of monogamous marriage can be understood within the framework of inclusive fitness theory. In this framework, the stability of monogamous marriage requires that men transfer property to their wife's offspring; consistently, the log-linear analysis of marriage and transfer strategies across a worldwide sample of societies shows that norms stipulating the transfer of land to wife's offspring exist in a larger proportion of monogamous than polygynous societies.

Secondly, phylogenetic comparative analyses of marriage and residence strategies across societies speaking Indo-European languages reconstruct early Indo-European society as practising monogamy and prevailing virilocality with alternative neolocality. However, there is no evidence of co-evolution of monogamy with neolocality in the history of these societies; thus, it cannot be excluded that the observed association between marriage and residence strategies is the artefact of a history of descent from a common ancestor.

In line with the archaeological, historical, and ethnographic evidence, these findings challenge explanations that link the emergence of monogamy and neolocality to the development of idiosyncratic features of "western" social organization; such explanations dominate the social sciences. More generally, they illustrate the relevance of the evolutionary paradigm to the study of kinship and marriage systems, contributing to the development of a biologically based social anthropology.

Acknowledgements

The work presented in this thesis benefited from contributions — in the form of comments, discussion, or encouragement — from Marco Archetti, Chloe Hodgkinson, Clare Holden, Fiona Jordan, Shakti Lamba, David Lawson, Ruth Mace, Andrew Meade, Mark Pagel, Rebecca Sear, and Stephen Shennan.

This work was funded through an ESRC 1+3 Research Studentship, a UCL Graduate School Research Scholarship, and a UCL Graduate School Research Scholarship for Cross-Disciplinary Training. Additional funding, mostly for travel, was provided by the AHRB Centre for the Evolutionary Analysis of Cultural Behaviour (CEACB), the AHRC Centre for the Evolution of Cultural Diversity (CECD), the UCL Department of Anthropology, the Fondazione Gini, and the UCL Graduate School.

I am grateful to Ruth Mace and Stephen Shennan for acting, respectively, as my primary and secondary supervisors, and to Andrew Pomiankowski for acting as my supervisor in the Department of Biology during the cross-disciplinary training year.

The modelling in Chapter 2 would not have happened without the patient help of Marco Archetti. The phylogenetic comparative analyses in Chapters 4 to 6 would not have happened had Mark Pagel and Andrew Meade not made available the BayesTraits package, advice on its use, and computer time on the ACET cluster. Together with Quentin Atkinson, they also made available the tree sample used for these analyses.

Many thanks to all in the office for tolerating the ever-growing piles of books and paper on and around my desk, and for offering kindness and support in return. Special thanks to Shakti Lamba for taking the time to comment on a near-final draft over a short period of time.

Most of all, and quite appropriately given the concern of the thesis, I am indebted to my family, for unfailing support throughout the years, and to Andrea Gobbo, for looking after me.

In memoriam VM

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Acronyms

EA *Ethnographic Atlas*

IE Indo-European

MCMC Markov chain Monte Carlo

MRCA most recent common ancestor

PIE Proto-Indo-European

PIH Proto-Indo-Hittite

RJ reversible jump

RJ-MCMC reversible jump Markov chain Monte Carlo

SCCS *Standard Cross-Cultural Sample*

Definitions

The definitions in this list apply throughout the thesis, unless otherwise specified. Where the terms are used with alternative meaning, this is stated explicitly in the text (e.g. the use of "monogamy" to designate a mating rather than marriage strategy).

Ambilocality Residence of married couple with or near the kin of either spouse.

Monogamy Marriage allowed to only one spouse at any one time.

Neolocality Residence of married couple apart from the kin of either spouse.

Polyandry Marriage allowed to multiple husbands simultaneously.

Polygamy Marriage allowed to multiple spouses simultaneously.

Polygyny Marriage allowed to multiple wives simultaneously.

Uxorilocality Residence of married couple with or near the wife's kin.

Virilocality Residence of married couple with or near the husband's kin.

Chapter 1

Introduction

1.1 Retrospect

In *The history of human marriage*, Westermarck (1921, p. 104) wrote

> Monogamy is the only form of marriage that is permitted among every people. Wherever we find polygyny, polyandry, or group-marriage, we find monogamy side by side with it. On the other hand, it is also in many cases the only form of marriage which is permitted by custom or law. This may be due to the mere force of habit ; or, possibly, to the notion that some men must not appropriate a plurality of wives when others in consequence can get none at all ; or to the feeling that polygyny is an offence against the female sex ; or to the condemnation of lust.

This excerpt, from the third volume of Westermarck's monumental opus, illustrates some of the problems that have plagued the anthropological study of kinship and marriage systems since its inception in the nineteenth century: for example, group-level norms are confounded with individual behaviour, such that variation in behavioural strategies within societies is contrasted with variation across societies. In the following decades, these difficulties precipitated the field into "a subject in which specialists talked only to each other (and some talked only to God)" (Fox 1983, p. 10). Couched in arcane language and obscure conceptual categories, its basic assumptions came under severe scrutiny during the second half of the twentieth century; by the end of the century, anthropology had essentially repudiated what it once viewed as its "basic discipline" (Fox 1967, p. 10; see discussion in Holy 1996, pp. 1–8).

As in other domains in the behavioural sciences (e.g. Gintis 2007; Mesoudi et al. 2006), evolutionary biology offers a unified conceptual and analytical framework to overcome these difficulties: after all, kinship and marriage systems represent "one form of assortative mating which has the interesting component of culturally defined categories" (Fox 1983, p. 3). Thus, the study of these features of social organization can capitalize on the suite of theoretical and methodological tools used in the analysis of social behaviour, both human and non-human (reviewed, respectively, in Dunbar and Barrett 2007b and in Krebs and Davies 1993); this suite includes tools used in the study of cultural behaviour, that is, behaviour that is acquired through social transmission (Richerson and Boyd 2005, p. 5; e.g. Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1981). In turn, to the extent that networks based on kinship and marriage created the social niche in which our species evolved, understanding their workings becomes crucial for understanding the evolution of human behaviour. Ultimately, a comprehensive evolutionary account of the human phenomenon must be able to explain why individuals organize relatedness and reproduction in the ways they do.

Anthropologists have generally resisted application of the evolutionary paradigm to the analysis of kinship and marriage systems, the classic complaint being that "social" and "biological" categories overlap but are not identical (Fox 1983, p. 3; e.g. Sahlins 1976). At the same time, with few notable exceptions (e.g. Hughes 1986, 1988), those advocating an evolutionary approach have generally failed to provide compelling explanations to account for these discrepancies. For example, one of the most powerful insights afforded by the evolutionary approach to the study of human behaviour is the asymmetry that characterizes sexually reproducing species, deriving from the higher potential rate of reproduction of males relative to females (see review in Brown et al. 2009). As discussed in Section 2.1, the cross-cultural prevalence of polygynous marriage is readily explained on this notion; why a small but substantial proportion of societies prescribe monogamous marriage is however not clear — mating is typically polygamous in these societies. The discrepancy between the "social" category of marriage and the "biological" category of mating would seem to disprove claims to the relevance of evolutionary explanations to these aspects of human social life.

The work presented in this thesis seeks to elucidate the relevance of the evolutionary paradigm to the study of kinship and marriage systems.

1.2 Prospect

In this section I provide a brief outline of the thesis (Section 1.2.1), followed by a discussion of conceptual and methodological issues arising from application of the evolutionary approach to the analysis of kinship and marriage systems; consideration of these issues guides the analyses in Chapters 2 to 6. I focus on the conceptualization of levels of explanation in Section 1.2.2 and on the statistical approaches used in cross-cultural analysis in Section 1.2.3.

1.2.1 Aims and structure of the thesis

In this thesis I investigate the evolution of kinship and marriage systems, addressing questions about their function, that is, their adaptive value in terms of differential reproduction, and about their history (Section 1.2.2). I focus on variation across societies in (i) *marriage strategies*, which specify how many spouses an individual may be married to at any one time, (ii) *transfer strategies*, which determine how resources are passed down the generations, and (iii) *residence strategies*, which regulate the pattern of sex-biased dispersal of individuals at marriage.[1]

In Chapter 2 I present a candidate model, in an inclusive fitness framework, for the evolution of monogamous marriage; in Chapter 3 I use cross-cultural data for a worldwide sample of societies to test the association between marriage and transfer strategies predicted by the theoretical analysis in Chapter 2. In Chapters 4 to 6 I use cross-cultural data on marriage and residence strategies for societies speaking Indo-European languages to reconstruct the pattern of change in these traits (Chapters 4 and 5) and their interactions (Chapter 6); the ethnographic context of these analyses is introduced in Section 1.2.3.2.

Each chapter includes a review of the relevant background and of research related to the specific case study, and a discussion of the findings. In Chapter 7 I discuss general themes emerging from the work in the preceding chapters.

[1]The notion of "strategic behaviour" in this context indicates "choice" between alternative forms of a given trait (Dunbar 2008, p. 132). I use this notion to designate "choice" at both the individual and the societal level: for example, males "choose" between the alternative strategies of monogamous and polygynous marriage in the analysis in Chapter 2, while societies "choose" between analogous alternatives in the analyses in Chapters 4 and 6. This usage is justified on the assumption that social norms emerge from the behavioural interactions of individuals over the generations, thereby capturing the outcomes of evolved inclusive-fitness-maximizing behaviours (Hughes 1988, p. 18; Section 1.2.2).

1.2.2 Levels of explanation

Investigating the evolution of a given behaviour involves asking questions about its function and about its history. In the analysis of kinship and marriage systems, we may ask why societies vary with respect to a particular set of norms, and how this variation came about — for example, why do some societies prescribe monogamous marriage, while the majority allow polygyny? Does the prevalence of this strategy among Eurasian societies reflect social or ecological determinants, or is it simply an artefact of history?

In Tinbergen's (1963) schema, these represent two of four levels at which we may aim to explain a given behaviour; the other two involve questions about the mechanisms, physiological or psychological, resulting in the behaviour, and questions about its ontogeny, that is, about the respective roles of genetic and environmental effects in this process — for example, what induces some men to take a second wife in societies that allow polygynous marriage, while other men settle for monogamy? Do men vary in the propensity to seek multiple sexual partners, and is this related to whether they engage in multiple marriages?

Function and history represent the ultimate causes of behaviour, mechanisms and ontogeny its proximate causes (Mayr 1961). The four levels of explanation are logically independent, in the sense that ignorance of the answer at one level does not preclude us from asking questions at another (Dunbar 2008, p. 132): alternative hypotheses compete within levels, not across them (Sherman 1988). Crucially, this implies that even though the process of cultural inheritance is known to operate through different dynamics than the process of genetic inheritance (e.g. Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1981), we can ask evolutionary questions about cultural behaviours without reference to the underlying mechanism of transmission (Dunbar and Barrett 2007a, p. 5). How a given behaviour is transmitted, whether genetically or through social learning, is a proximate question (West et al. 2007b).[1]

Of course, full understanding of any phenomenon requires answers at all levels of explanation; for humans, as for other species with social transmission of behaviour,

[1]Within this framework, understanding the interactions between the processes of genetic and cultural evolution has been characterized as answering proximate questions about human behaviour (e.g. Henrich and McElreath 2003), or as answering both proximate and ultimate questions (e.g. Richerson and Boyd 2005).

this involves taking into account both genetic and cultural evolution (Rogers 1988; see Laland 2008 for discussion of the issue of non-human culture). One key advantage of starting by addressing ultimate questions is that it forces us to treat human behaviour in the general terms used to characterize the behaviour of other species; this, in turn, forces us to think *explicitly* about where and how our species departs from the predictions of the "biological" paradigm. Approaches that focus on the proximate determinants of human behaviour typically sidestep this crucial issue (Henrich and McElreath 2003; West et al. 2007b). Further, placing kinship and marriage systems in the wider context of animal social behaviour provides a set of first principles for devising analytical traits and categories that are theoretically justifiable and empirically useful. This is crucial for clearing up the terminological confusion that has dominated the study of kinship and marriage systems within anthropology, eventually leading to its demise (Section 1.1), and which has fostered more confusion in other fields that have relied on previous anthropological theorizing (see for instance Sections 5.1 and 5.4).

For example, the analysis in Chapter 2 asks under what conditions monogamous marriage can maximize inclusive fitness where fitness is linked to resources and resources are transferred across generations. Of course, variation in marriage strategies across societies, or in other features of social organization, is unlikely to be based on genetic differences (Hughes 1988, pp. 6–7). The inclusive fitness metaphor is used in this case as shorthand for the assumption that social norms effect the "biological" paradigm; that is, that they encode the cumulative outcomes of the inclusive-fitness-maximizing behavioural tendencies of individuals (Alexander 1979b, p. 68). Irrespective of its validity, this assumption represents a useful starting point for investigating the complexity of human social systems, at least to the extent that it helps us conceptualize previous anthropological observations about the distribution of marriage strategies, and that it focuses further empirical work in this area (see for instance Sections 2.4 and 3.1). Next, we can ask through what proximate mechanisms these inclusive-fitness-maximizing behavioural tendencies are realized. For example, in societies with status differentiation based on ownership of resources, monogamous marriage and the transfer of property to lineal heirs may reflect the conscious concern of individuals with the preservation of status through the concentration of wealth (Rogers 1995; e.g. Goody 1976, discussed in Section 3.1.2); status and ownership of resources are typically linked to fitness in these societies (see review in Hopcroft 2006; e.g. Nettle and Pollet 2008).

Finally, we can ask to what degree the process of cultural evolution can lead to patterns of behaviour that are inconsistent with the predictions of the "acultural" model (Rogers 1988). For instance, we can investigate how the evolutionary dynamics are affected by proximate considerations relating to the transmission of mating preferences or of norms regulating sexual behaviour (e.g. Mesoudi and Laland 2007). Importantly, these specific questions about human social life become meaningful only within the wider context of variation in animal social behaviour.

1.2.3 Cross-cultural analysis

To the extent that kinship and marriage systems determine the structure of human societies, they likely played a key part in the unfolding of history. At the same time, long-term population processes such as migration and diffusion likely shaped the observed pattern of variation in kinship and marriage systems. Unravelling the interactions between these facets of history becomes crucial for understanding the evolution of human social organization, and of human behaviour more generally (Jones 2003; e.g. Gamble 2008; Gowlett 2008).

However, the statistical analysis of variation in cultural traits across societies presents a major methodological issue: some societies are more closely related than others, either by way of descent from a common ancestor or through contact. Consequently, the assumption of independence of sample units is untenable for any cross-cultural dataset (Dow 1993). Kinship and marriage systems appear to be "conservative" features of social organization (Murdock 1949, p. 196); in the context of linguistic and genetic variation, the effect of descent is strongest at the supra-regional level, while the effect of contact prevails within regions (Borgerhoff Mulder et al. 2001, 2006; Burton et al. 1996; Guglielmino et al. 1995; Hewlett et al. 2002; Holden and Mace 1999; Jones 2003; Moylan et al. 2006).

The issue of the non-independence of sample units in cross-cultural analysis was first recognized by Galton in response to the earliest application of statistical methods to cross-cultural data, Tylor's (1889) study of norms relating to marriage and descent (Jorgensen 1979). I employ two strategies to address "Galton's problem": use of Murdock and White's (1969) *Standard Cross-Cultural Sample* in Chapter 3 (Section 1.2.3.1) and of phylogenetic comparative methods in Chapters 4 to 6 (Section 1.2.3.2).

1.2.3.1 The *Standard Cross-Cultural Sample*

Murdock and White (1969) collated the *Standard Cross-Cultural Sample* (*SCCS*) with the aim to adequately represent the range of known cultural variation (that is, avoiding biases towards regions that are overrepresented in the ethnographic record), while *minimizing* the effects of descent and contact on the distribution of cultural practices (Murdock 1977). To these ends, Murdock (1963b, 1966, 1967b, 1968) had previously divided entries in the *Ethnographic Atlas* (*EA*) into sets including societies that he believed to share similarities through descent and/or contact (see discussion in Jorgensen 1979).[1] From each set, Murdock and White (1969) sought to include in the *SCCS* the society with the most extensive coverage; in any case, they excluded entries that could not be focused ("pinpointed") to a specific date and locality of observation. This strategy produced a sample including 186 societies; empirical estimates indicate that it was successful in reducing the degree of non-independence within the sample (Dow 1989, 1993; Dow and Eff 2008; Murdock and White 1969), and in reducing the amount of random error that derives from the use of non-focused data (Divale 1975). Finally, by establishing a standard sample, Murdock and White (1969) aimed to facilitate integration of data and findings across studies. Currently, the *SCCS* codebook boasts coded data for approximately 2000 variables (White et al. n.d.); for comparison, the *EA* codebook includes coded data for approximately 100 variables for the 1267 societies in the sample (Gray 1999).

The quality and quantity of the *SCCS* data, combined with the reduction in the degree of non-independence, make use of this sample the strategy of choice when alternative approaches to cross-cultural comparison are not applicable (Gray 1996). For example, phylogenetic comparative methods control for, rather than merely minimize, the non-independence of societies, but their application becomes problematic when the traits of interest show limited variation within language families (Section 1.2.3.2). I use the phylogenetic comparative approach for the analyses in Chapters 4 to 6, but resort to using the *SCCS* for the analysis in Chapter 3 because the traits under investigation in this chapter (marriage and transfer strategies) show limited variation within the sample of Indo-European-speaking societies analysed in Chapters 4 to 6. Further, in Chapter 3 I aim to control for the effect of religious affiliation on the distribution of marriage and

[1] The *EA* is a collection of coded ethnographic data published in instalments in the journal *Ethnology*, starting with Murdock (1962) and summarized in Murdock (1967a,b).

transfer strategies, and multivariate analysis is not implemented by the phylogenetic comparative method used in Chapters 4 to 6. To give a concrete example of the scale of analysis afforded by the *SCCS* (Section B.1), the twenty monogamous societies included in the analysis in Chapter 3 are spread across all continents and speak languages belonging to ten families and three isolates, with no more than three speaking languages belonging to the same family. The three monogamous Indo-European-speaking societies included in the analysis — Irish (Celtic sub-group), Armenians (Armenian sub-group), and Punjabi (Indo-Iranian sub-group) — last shared a common ancestor 7300 years BP (Gray and Atkinson 2003).

In any case, since clustering of variables still obtains in the *SCCS*, both by language family and by region (Dow 1989, 1993; Dow and Eff 2008; Eff 2004; Murdock and White 1969; Murdock et al. 1978), results derived from analysis of this sample are best taken as suggestive rather than as conclusive.

1.2.3.2 The phylogenetic comparative approach

Like human societies, species and other biological taxa are hierarchically related by way of descent from a common ancestor. Evolutionary biologists employ phylogenetic comparative methods to control for the resulting non-independence in analyses of attributes across taxa (Felsenstein 1985; Harvey and Pagel 1991). Using a phylogenetic tree to represent how the taxa are related, these methods infer likely evolutionary scenarios that produced the observed distribution of the attribute(s) of interest across the taxa. Besides testing for correlated evolution between traits, they can be used to infer evolutionary pathways, to estimate rates of evolutionary change, and to reconstruct ancestral states of the traits (see review in Felsenstein 2004, Chapter 25).

Mace and Pagel (1994) advocated the use of phylogenetic comparative methods in cross-cultural analysis, to control for the component of non-independence resulting from the descent of societies from a common ancestor. The component resulting from contact comprises instances of "horizontal transmission" of traits across societies, for example through copying. Societies lose or acquire cultural traits either through original invention or through horizontal transmission; both represent pathways through which functional associations between traits can arise. However, phylogenetic comparative methods assume that traits are transmitted vertically, i.e. from parent to daughter populations, along the branches of the phylogenetic tree model used to represent how

the taxa are related; consequently, high rates of horizontal transmission may invalidate their application to cross-cultural data (Borgerhoff Mulder 2001; Borgerhoff Mulder et al. 2006; Nunn et al. 2006; Rogers and Cashdan 1997). Yet high rates of horizontal transmission, in a process of "cultural infection" (Mace 2005, p. 203) where two or more traits spread together across societies even though they are not functionally related, are by definition problematic for *any* method used in cross-cultural research, since the basic assumption of cross-cultural hypothesis testing is that traits tend to occur together if they are functionally related (Murdock and White 1969). By contrast, phylogenetic comparative methods outperform non-phylogenetic methods under a wide range of simulated scenarios and levels of horizontal transmission (Currie et al. submitted; Nunn et al. 2006). In Section 3.4 I discuss the "cultural infection" scenario in relation to the spread of monogamous marriage alongside Christianity.

The analyses in Chapters 4 to 6 use a phylogenetic comparative method in a Bayesian reversible jump (RJ) Markov chain Monte Carlo (MCMC) framework (Pagel and Meade 2005, 2006; Pagel et al. 2004). The Bayesian MCMC framework uses a single tree or a sample of trees to represent how the taxa are related; use of a tree sample removes dependence of the inferences upon any single phylogenetic hypothesis (Section 4.1.2). This is particularly important for application of the phylogenetic approach to cross-cultural data, since the reticulate nature of the interactions linking human societies cannot be captured by any single tree model (see discussion in Bellwood 1996). In a similar way, the RJ-MCMC implementation of the approach removes dependence of the inferences upon any single model of trait evolution; the model of trait evolution specifies, for example, whether a trait is likely to be acquired and lost at the same or at different rates. This is also crucial in the analysis of cultural traits, because the mechanisms of trait change are usually unknown in this case. More generally, the Bayesian MCMC framework estimates the degree of statistical uncertainty in the parameters of interest to the comparative question (e.g. in the rates of trait change); this provides an indication of the degree of confidence that can be placed in any particular inference about the evolution of the trait(s).

Language trees as history Single trees representing human population history for use in phylogenetic comparative analyses can be derived from application of phylogenetic tree-building methods to linguistic data (e.g. Fortunato and Mace 2009;

Holden and Mace 2003); samples of trees can be derived from application of these methods to linguistic data in a Bayesian MCMC framework (e.g. Fortunato et al. 2006; Jordan et al. 2009).

To date, the phylogenetic tree-building approach has been applied to Austronesian (Gray et al. 2009; Gray and Jordan 2000), Bantu (Holden 2002; Holden et al. 2005; Rexová et al. 2006), Indo-European (Gray and Atkinson 2003; Rexová et al. 2003; Ringe et al. 2002), Papuan (Dunn et al. 2005), and Semitic (Kitchen et al. 2009) languages, and has proven extremely successful in recovering human population history. This approach is in fact intuitively close to the traditional comparative method of historical linguistics (Atkinson and Gray 2005; Gray et al. 2007; Pagel 2009): both aim to reconstruct the relationships among a set of languages, based on the similarities and differences in lexical or structural features, and both model the relationships as branching rooted trees, with internal nodes representing ancestral entities. Unlike the traditional linguistic approach, however, the computational methods employed in phylogenetic tree-building analysis make use of explicit criteria to choose among the host of possible tree topologies — a non-trivial issue considering that, for instance, the number of possible configurations is in the order of $5 \cdot 10^{38}$ for a sample of 30 languages (Felsenstein 2004, p. 24). Further, methods are available within the computational approach that enable visualization of the degree to which linguistic relationships can be modelled as a tree rather than as a network (e.g. Bryant et al. 2005; Holden and Gray 2006; Nakhleh et al. 2005). For example, the basic vocabulary of Indo-European languages appears "strikingly tree-like" (Bryant et al. 2005, p. 81) in these visualization exercises (Atkinson et al. 2005; Bryant et al. 2005); basic vocabulary includes items of vocabulary such as pronouns, body parts, and numerals, which are less prone to innovation and borrowing (i.e. horizontal transmission) than other meanings (Section 4.2.2). The ability to visualize conflicting signal caused by horizontal transmission of the linguistic traits (e.g. words) used to build the trees addresses concerns that tree models may be inappropriate given the reticulate nature of the interactions linking human societies (e.g. Bateman et al. 1990; Boyd et al. 1997; Moore 1994). In any case, Bayesian MCMC phylogenetic tree-building methods are robust to a wide range of simulated scenarios and levels of horizontal transmission of the linguistic traits used to build the trees (Greenhill et al. 2009).

Following traditional linguistic practice, most phylogenetic tree-building analyses have used vocabulary data, which allow for time depths of approximately 8000 ± 2000 years (Gray 2005); relationships resulting from over 10,000 years of divergence can be inferred from structural features, such as grammar and sound systems, but the relevant data are currently available only for a small number of languages (e.g. Dunn et al. 2005). As a result, phylogenetic comparative analyses that use language trees generated through computational methods are currently limited to the language family level; as noted in Section 1.2.3.1, this can become problematic when the traits of interest show limited variation within language families. The temporal reach of the phylogenetic comparative approach can be extended beyond this level of analysis using multifamily trees derived from the linguistic literature (e.g. Holden and Mace 1997, 1999); however, this strategy forgoes the advantages of using a sample of trees, as opposed to a single tree, within the Bayesian phylogenetic comparative framework.[1]

Ethnographic focus The tree sample used in the analyses in Chapters 4 to 6 was generated by Pagel et al. (2007) through application of a phylogenetic tree-building method, in a Bayesian MCMC framework, to Indo-European (IE) basic vocabulary data collated by Dyen et al. (1992) (Section 4.2.2). In previous analyses of these data, Gray and Atkinson (2003) used the same approach to test between the two main competing hypotheses for the origin of the IE language family (see also Atkinson et al. 2005; Atkinson and Gray 2006a,b); they found support for the scenario proposed by Renfrew (1987), which posits the expansion of IE languages from Anatolia with the spread of agriculture beginning around 7000 to 6000 BCE (Diamond and Bellwood 2003). The alternative hypothesis, proposed by Gimbutas (1973a,b), places the homeland of the language family in the Pontic steppes north of the Black Sea, and envisages an

[1] In principle, the use of gene trees as models of population history in phylogenetic comparative analyses lifts the time and language family constraints imposed by the use of language trees generated through computational methods (e.g. Holden and Mace 1997, 1999, for the use of molecular trees obtained from the genetic literature). By using samples of trees generated from application of Bayesian MCMC phylogenetic tree-building methods to molecular data, this approach would at the same time enable implementation of the Bayesian phylogenetic comparative framework.

In practice, however, the use of gene trees as models of population history is problematic because of the widespread discordance between the topologies of trees recovered from analysis of different genes; this issue is currently being addressed through the development of multilocus approaches to phylogenetic tree-building (see review and discussion in Degnan and Rosenberg 2009).

expansion driven by nomadic horse-riding pastoralists starting after 4000 BCE (Diamond and Bellwood 2003).

Reconstructions of early IE social structure based on cross-cultural data have been used in archaeology and linguistics to support the latter scenario, but this practice has been marred by substantial methodological flaws and bias in interpretation (Sections 4.1 and 5.1). The reconstructions of early IE marriage and residence strategies in Chapters 4 and 5, obtained from application of the phylogenetic comparative approach to cross-cultural data, provide an independent line of evidence against which to evaluate previous inferences about early IE social structure. In turn, reconstructing the historical processes that shaped variation in these traits across IE-speaking societies, as well as their interactions (Chapter 6), is crucial for evaluating theoretical claims to the centrality of the "nuclear family" to European, and indeed to "western", social organization; such claims abound in the social sciences, typically outside anthropological circles (Goody 1996; Smith 1993).[1] To put it with Fox (1997, p. x), 'Sociology ... [got] bogged down in something called "the family" and an enterprise of "family sociology" that was indeed the pursuit of a cultural construct rather than a cultural universal'; analogous considerations can be extended to economics and demography. It is in the search of these universals that anthropology and evolutionary approaches to the study of kinship and marriage, combined, can offer the greatest contribution to our understanding of human social behaviour.

[1] In anthropology, the "nuclear family" designates a family unit comprising parents and their dependent children (Fox 1983, p. 36; Keesing 1975, p. 150; Parkin 1997, p. 28); technically, therefore, nuclear families exist in societies practising monogamous and polygamous marriage (Murdock 1949, pp. 1–2; see discussion in Fox 1983, pp. 36–40). Typically outside anthropology, as well as in everyday parlance, this concept is used rather vaguely to designate the small isolated (i.e. monogamous and non-extended) family type characteristic of "western" social organization (e.g. Smith 1993); throughout the thesis, I enclose instances of this usage in quotes.

Chapter 2

Evolution of monogamous marriage by maximization of inclusive fitness

2.1 Introduction

Eighty-three percent of human societies allow polygynous marriage (Murdock and White 1969; Murdock and Wilson 1972). In humans, as in other sexually reproducing species, the lower investment in gametes by males leads to the higher potential rate of reproduction of individual males relative to individual females. This, coupled with proximate constraints such as internal gestation and lactation, produces the typical mammalian pattern of polygynous breeding, characterized by high male investment in mating effort and high female investment in parental effort (Clutton-Brock and Vincent 1991; Trivers 1972). Extension of this paradigm to human social systems is used to explain the cross-cultural prevalence of polygynous marriage (e.g. Low 2003, 2007; Marlowe 2003). In some societies that allow polygynous marriage the majority of men may be each married to a single wife, because few command sufficient skill or resources to marry polygynously (White 1988). This marriage pattern, sometimes referred to as "monogamy" (e.g. Marlowe 2003), is common among foragers and likely evolved because of the benefits of biparental care to offspring survival (Low 2003, 2007).

Adapted from a manuscript in press as Fortunato, L. and Archetti, M. Evolution of monogamous marriage by maximization of inclusive fitness. *Journal of Evolutionary Biology.*

This is distinct from the system of social monogamy found in the remaining 17% of societies, in which polygynous marriage is forbidden or disapproved (Murdock and White 1969; Murdock and Wilson 1972). Current evolutionary explanations view this marriage strategy as a mechanism of reproductive levelling (e.g. Alexander 1987; Alexander et al. 1979; Bowles et al. 2003). A system of "socially imposed monogamy" (Alexander et al. 1979, p. 420) would reduce within-group competition by suppressing differences in reproductive success among men. Because of the attendant increase in within-group co-operation, societies adopting this strategy would have an advantage in competition with other groups. This would enable the cohesion of increasingly larger societies, ultimately leading to the formation of large nations (Alexander et al. 1979, pp. 423, 432–433; Alexander 1987, pp. 71–73). However, social monogamy long predates the establishment of large nation states (Herlihy 1995): while the diffusion of norms prescribing monogamous marriage is commonly attributed to the spread of Christianity, restrictions on polygynous marriage appear in the earliest historical records (Westermarck 1921, p. 104; Section 3.4). For instance, Babylonian men were legally entitled to an additional wife only under special circumstances, such as illness or infertility of the first (as documented by the *Codex Hammurabi*, early second millennium BCE); strict monogamy was the only legally recognized form of marriage in ancient Greece and Rome (Herlihy 1995; Scheidel 2009). More importantly, the "socially imposed monogamy" model rests on the assumption that monogamous marriage significantly reduces the variance in male reproductive success (Alexander et al. 1979, p. 420). However, the historical and ethnographic evidence show that dominant individuals invariably attain extraordinary reproductive success even where marriage is strictly monogamous (Herlihy 1995; Low 2003; Scheidel 2009). Ancient Rome is a case in point: despite the fanatical prescription of monogamous marriage, wealthy men fathered children by large numbers of slave women (Betzig 1992a,b; Herlihy 1995; Scheidel 2009).[1]

[1] Consistently, across data for 18 modern populations collated by Brown et al. (2009) we found no significant difference in variance in male reproductive success between societies practising monogamous marriage ($n = 6$, median: 10.0, range: 2.3–23.6) and societies practising polygynous marriage ($n = 12$, median: 10.4, range: 8.1–24.4) (Mann-Whitney U = 27.00, $z = -0.84$, n.s., $r = -0.20$. We coded societies on marriage strategy based on information in the original references in Brown et al. 2009, or references therein; our coding corresponds to the mating system coding in Brown et al. 2009, except for the Pimbwe, Dobe !Kung, and Ache, which we coded as practising polygynous marriage).

Here we develop an inclusive fitness model to conceptualize variation in marriage strategies across societies, and show that the evolution of monogamous marriage can be understood within the framework of inclusive fitness theory (Hamilton 1964a,b). We proceed in three steps. In the remainder of this section, we identify two candidate factors that can make social monogamy advantageous over alternative marriage strategies. In Sections 2.2 and 2.3 we develop a game-theoretic model to show that these factors can indeed result in monogamous marriage as a stable evolutionary strategy. Finally, in Section 2.4 we discuss previous anthropological observations on the history and cross-cultural distribution of marriage strategies in the context of the model.

Evolutionary accounts of marriage strategies typically assume that male reproductive success is constrained by access to females (e.g. Pollet and Nettle 2009). However, in traditional human societies where individuals hold rights to property, inherited wealth is a key determinant of reproductive success (see review in Hopcroft 2006), and reproductive opportunities may be constrained more by ownership of resources than by access to mates. In these societies, individuals are expected to transfer resources across generations in ways that maximize the effect of the resources on their inclusive fitness (Hrdy and Judge 1993; Rogers 1990). To the extent that there is a trade-off between transmitting genes and transmitting wealth to the next generation (Rogers 1990), in some cases the optimal strategy may be to concentrate resources in a limited number of heirs. By definition, social monogamy channels a man's property to the offspring of a single wife; additionally, unigeniture (e.g. primo- or ultimogeniture) may be used to avoid partitioning resources among them. In contrast, the property of a polygynous man is typically divided among his wives' offspring (although unigeniture may apply *within* sets of siblings by the same mother) (Goody 1976; Gray 1964; Mair 1971). This suggests that social monogamy may be advantageous where partitioning of resources causes a depletion of their fitness value.

But in humans, as in other sexually reproducing species, the reproductive interests of individuals in a socially monogamous pair only coincide if the male is the biological father of the female's offspring (Alexander 1987, p. 70). Therefore, males need to balance the benefit of investing in closely related heirs with the risk of investing in someone else's offspring. If a man has a low probability of being the biological father of his wife's children, he may be better off investing in his sister's: relatedness to a sister is always certain (through one's mother), as is relatedness to her offspring

(Alexander 1974; Greene 1978). In fact, the transfer of a man's property to his sister's sons is common in societies with frequent female extramarital sex (Flinn 1981; Hartung 1981). We extend this reasoning to incorporate the strategic behaviour of females: if natural selection favours males who allocate resources based on their level of paternity, in turn it may favour females who allocate paternity based on the degree of male investment in their offspring. The resulting trade-off between paternity and investment of resources may lead to social monogamy: males would benefit from increased levels of paternity in their wife's offspring, and females from exclusive investment of their husband's resources in their own offspring. Of course, this mechanism can only operate if males have cues about paternity. In humans, in addition to direct phenotypic cues (see review in Geary 2006), indirect behavioural cues may include the conformity of females to norms regulating their sexual behaviour; such norms are found in the vast majority of societies (Broude and Greene 1976).

2.2 Theoretical framework

We capture these intuitive arguments with a game-theoretic model, described in detail in Section A.1. We focus on a population in which both males and females marry either monogamously or polygamously, with $w \geq 1$ wives for males and $h \geq 1$ husbands for females. Males transfer resources to the next generation "vertically" to their wives' offspring or "diagonally" to their sister's offspring (Figure 2.1). Females produce one male and one female offspring; each sibling pair inherits resources δ from the parent generation, with $\delta = \delta_{\mathrm{m}} + \delta_{\mathrm{f}} = 1$ in a monogamous population in which all males transfer vertically, and $0 \leq \delta_{\mathrm{m}} \leq 1$ and $0 \leq \delta_{\mathrm{f}} \leq 1$ the male and female contributions to δ. The fitness of each sibling pair is given by δ^z, with $z > 0$, where z describes the relationship between inherited resources and fitness; for $z > 1$, the fitness value of δ is depleted when δ is partitioned among the offspring of multiple wives.

The probability p that a male is the biological father of his wife's offspring depends on the behaviour of females, who give their husbands either "high" paternity p_{H} or "low" paternity p_{L}, with $0 < p_{\mathrm{L}} < p_{\mathrm{H}} \leq 1$. Females obtain an additional generic advantage α from mating with other males besides their husbands, with $\alpha_{\mathrm{L}} > \alpha_{\mathrm{H}}$, and $\alpha_{\mathrm{H}} = 0$ for $p_{\mathrm{H}} = 1$. Males can infer their level of paternity from phenotypic or behavioural cues.

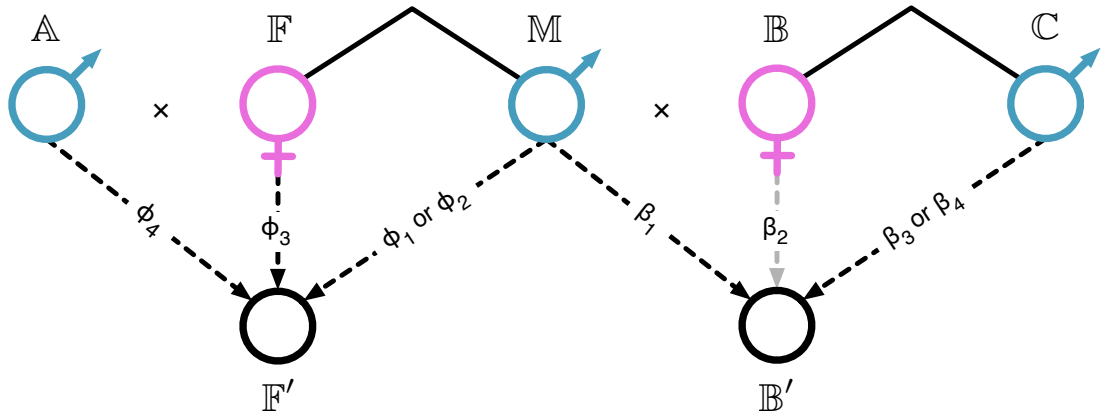


Figure 2.1: Inclusive fitness contributions for a focal male $\mathbb{M}$ and a focal female $\mathbb{F}$. In the parent generation crosses represent marriages, solid lines represent brother–sister relationships ($\mathbb{A}$: $\mathbb{F}$'s husband; $\mathbb{B}$: $\mathbb{M}$'s wife; $\mathbb{C}$: $\mathbb{B}$'s brother). In the offspring generation $\mathbb{B}'$ and $\mathbb{F}'$ each represent a sibling pair ($\mathbb{B}'$: $\mathbb{B}$'s offspring; $\mathbb{F}'$: $\mathbb{F}$'s offspring). Dashed arrows represent resource transfers from parent to offspring generation. β_i represents resources transferred to $\mathbb{B}'$ (β_1 if $\mathbb{M}$ transfers vertically; β_2 if $\mathbb{B}$ is polyandrous and her other husbands, excluding $\mathbb{M}$, transfer vertically; β_3 if $\mathbb{C}$ does not marry; β_4 if $\mathbb{C}$ marries and transfers diagonally); β_2 is grey to indicate that the resources are transferred by $\mathbb{B}$'s husbands other than $\mathbb{M}$ (which are not shown), rather than by $\mathbb{B}$ herself. ϕ_i represents resources transferred to $\mathbb{F}'$ (ϕ_1 if $\mathbb{M}$ does not marry; ϕ_2 if $\mathbb{M}$ marries and transfers diagonally; ϕ_3 if $\mathbb{F}$ does not marry; ϕ_4 if $\mathbb{F}$ marries and $\mathbb{A}$ transfers vertically). See Section A.1 for details.

Schematically, the inclusive fitness payoff for a focal male $\mathbb{M}$ in the parent generation is given by the fitness value of resources β_i, inherited by the offspring $\mathbb{B}'$ of his $\mathring{w} \geq 1$ wives, plus the fitness value of resources ϕ_i, inherited by his sister's offspring $\mathbb{F}'$, each scaled by the respective coefficient of relatedness ($r_{\mathbb{MB}'}$ or $r_{\mathbb{MF}'}$) (Figure 2.1 and Table 2.1). The subscript $i = 1, \ldots, 4$ denotes the pathway through which resources are transferred to the heir, as per Figure 2.1. $\mathring{w} \neq w$ for a mutant focal male whose marriage strategy differs from the strategy of resident males, and $\mathring{w} = w$ in all other cases. Resources are divided equally among the male's wives' offspring. This can be written as

$$E_{\mathbb{M}} = \mathring{w}\left(\frac{\beta_1 + \beta_2 + \beta_3 + \beta_4}{\mathring{w}}\right)^z r_{\mathbb{MB}'} + (\phi_1 + \phi_2 + \phi_3 + \phi_4)^z r_{\mathbb{MF}'}.$$

Similarly, the inclusive fitness payoff for a focal female $\mathbb{F}$ is given by the fitness value of resources β_i, inherited by the offspring $\mathbb{B}'$ of her brother's w wives, plus the fitness value of resources ϕ_i, inherited by her offspring $\mathbb{F}'$, each scaled by the respective coefficient of relatedness ($r_{\mathbb{FB}'}$ or $r_{\mathbb{FF}'}$), plus any advantage $\mathring{\alpha}$ she obtains from mating with other males besides her husbands (Figure 2.1 and Table 2.1). As in the previous case, the subscript $i = 1, \ldots, 4$ denotes the pathway through which resources are transferred to the heir, as per Figure 2.1. $\mathring{\alpha} \neq \alpha$ for a mutant focal female whose paternity strategy differs from the strategy of resident females, and $\mathring{\alpha} = \alpha$ in all other cases. This can be written as

$$E_{\mathbb{F}} = w\left(\frac{\beta_1 + \beta_2 + \beta_3 + \beta_4}{w}\right)^z r_{\mathbb{FB}'} + (\phi_1 + \phi_2 + \phi_3 + \phi_4)^z r_{\mathbb{FF}'} + \mathring{\alpha}.$$

The possible combinations of male and female strategies differ in inclusive fitness payoffs; given these payoffs, we can derive evolutionarily stable equilibria consisting of a pair of male and female strategies that cannot be invaded by rare mutants playing alternative strategies (Maynard Smith 1982; Section A.2).

2.3 Results

Social monogamy is a stable evolutionary outcome under two scenarios (Section A.2 and Table A.1); both require "suspicious" males, that is, males who transfer vertically if females are monogamous and provide "high" paternity, diagonally otherwise. In the first scenario females always provide "high" paternity. In the second scenario

Table 2.1: Symbols used in the inclusive fitness payoffs

Symbol*		Focal individual	
		$\mathbb{M}$	$\mathbb{F}$
Resource transfers to $\mathbb{B}'$ (β_i)	β_1	$\Omega\,\mathring{m}_{\mathrm{V}}[\delta_{\mathrm{m}} + \mathring{w}\,(\delta_{\mathrm{f}}/h)]$	$\Omega\,m_{\mathrm{V}}[\delta_{\mathrm{m}} + w\,(\delta_{\mathrm{f}}/h)]$
	β_2	$\Omega\,\mathring{w}\,m_{\mathrm{V}}(h-1)(\delta_{\mathrm{m}}/w + \delta_{\mathrm{f}}/h)$	$\Omega\,w\,m_{\mathrm{V}}(h-1)(\delta_{\mathrm{m}}/w + \delta_{\mathrm{f}}/h)$
	β_3	$\Omega\,\mathring{w}\,(1-\Omega)\delta_{\mathrm{m}}$	$\Omega\,w\,(1-\Omega)\delta_{\mathrm{m}}$
	β_4	$\Omega\,\mathring{w}\,\Omega\,m_{\mathrm{D}}[\delta_{\mathrm{m}} + w\,(\delta_{\mathrm{f}}/h)]$	$\Omega\,w\,\Omega\,m_{\mathrm{D}}[\delta_{\mathrm{m}} + w\,(\delta_{\mathrm{f}}/h)]$
Resource transfers to $\mathbb{F}'$ (ϕ_i)	ϕ_1	$(1-\Omega)\delta_{\mathrm{m}}$	$(1-\Omega)\delta_{\mathrm{m}}$
	ϕ_2	$\Omega\,\mathring{m}_{\mathrm{D}}[\delta_{\mathrm{m}} + \mathring{w}\,(\delta_{\mathrm{f}}/h)]$	$\Omega\,m_{\mathrm{D}}[\delta_{\mathrm{m}} + w\,(\delta_{\mathrm{f}}/h)]$
	ϕ_3	$(1-\Phi)\delta_{\mathrm{f}}$	$(1-\Phi)\delta_{\mathrm{f}}$
	ϕ_4	$\Phi\,h\,m_{\mathrm{V}}(\delta_{\mathrm{m}}/w + \delta_{\mathrm{f}}/h)$	$\Phi\,\mathring{h}\,\mathring{m}_{\mathrm{V}}(\delta_{\mathrm{m}}/w + \delta_{\mathrm{f}}/\mathring{h})$
Coefficients of relatedness (r_{xy})	to $\mathbb{B}'$	$[\mathring{p} + (h-1)p]/2h^2$	$(p/2h)[(1+p^2/h)/4]$
	to $\mathbb{F}'$	$(1/2)[(1+p^2/h)/4]$	$1/2$

* The subscript $i = 1, \ldots, 4$ to β and ϕ denotes the pathway through which resources are transferred to the heir, while the subscripts to r denote the focal individual x ($\mathbb{M}$ or $\mathbb{F}$) and heir y ($\mathbb{B}'$ or $\mathbb{F}'$), as per Figure 2.1. Ω denotes the marriage probability for males, Φ the marriage probability for females. m_{V} denotes the probability that a male transfers vertically, $m_{\mathrm{D}} = 1 - m_{\mathrm{V}}$ the probability that he transfers diagonally. $\mathring{}$ indicates any attribute that may depend on the relevant strategy for the focal individual, such that its value may differ from the corresponding value for the resident population. See Section A.1 for details.

Table 2.2: Conditions for the stability of "suspicious" monogamous males for $p_{\mathrm{H}} = 1$

Notation*	Condition†	Strategy of mutant males
a	$z < \log 3 / \log 2$	Monogamous marriage with diagonal transfer
b‡	$w_{\mathrm{P}}(\delta_{\mathrm{m}}/w_{\mathrm{P}} + \delta_{\mathrm{f}})^z p_{\mathrm{L}} < 1$	Polygynous marriage with vertical transfer
c	$(2\delta_{\mathrm{m}} + \delta_{\mathrm{f}} + w_{\mathrm{P}}\delta_{\mathrm{f}})^z < 3$	Polygynous marriage with diagonal transfer

* Corresponds to the labels used in Figure 2.2a. See Section A.2 for details.

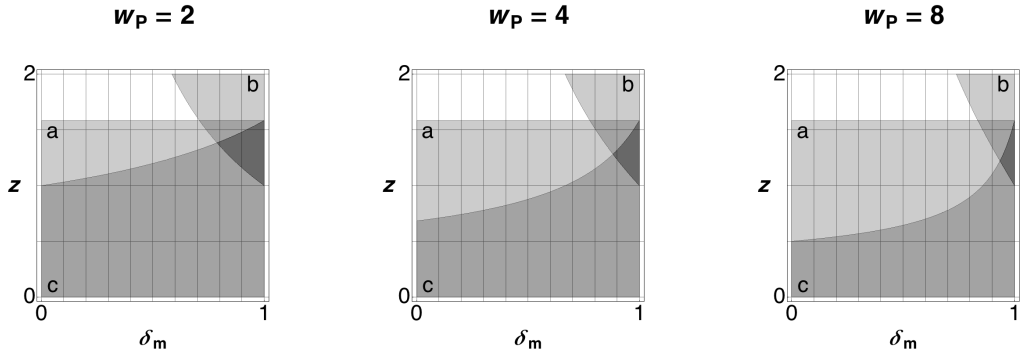
† $w_{\mathrm{P}} > 1$ denotes the number of wives for a polygynous male.

‡ $p_{\mathrm{L}} = 1$ with females who always provide "high" paternity.

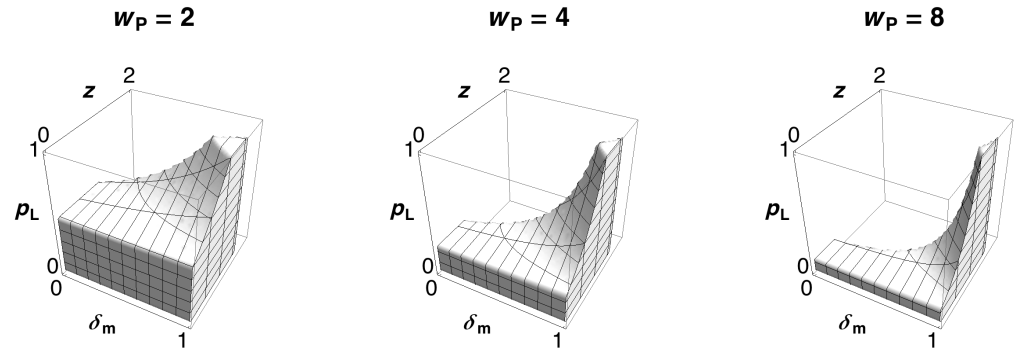
females are "astute", that is, they provide "high" paternity if males are monogamous, "low" paternity otherwise. Both combinations of male and female strategies result in monogamous marriage, vertical transfer, and "high" paternity.

Figure 2.2 illustrates the two scenarios for $p_{\mathrm{H}} = 1$. In the first case, monogamy can be advantageous where there is a fitness cost to dividing resources among the offspring of multiple wives (i.e. for $z > 1$; condition **b** in Table 2.2; Figure 2.2a). In the second case, because of the strategic behaviour of females, polygynous males suffer a reduction in relatedness to wives' offspring; consequently, monogamy can be advantageous irrespective of whether the fitness value of resources is depleted through division (i.e. for $z > 0$; condition **b** in Table 2.2; Figure 2.2b). Vertical transfer can be advantageous where the benefit to a man of providing extra resources to his sister's offspring is offset by their lower relatedness relative to wife's offspring (i.e. for z below the threshold specified by condition **c** in Table 2.2; Figures 2.2a and 2.2b). Monogamy and vertical transfer become increasingly advantageous as each wife provides a relatively smaller share of the resources inherited by her offspring (i.e. as δ_{m} increases and/or w_{P} decreases; conditions **b** and **c** in Table 2.2; Figures 2.2a and 2.2b). Additionally, in the second case the benefit to monogamy increases as the relatedness between a polygynous male and his wives' offspring decreases (i.e. as p_{L} decreases; for $p_{\mathrm{L}} < 1/w_{\mathrm{P}}$, any potential fitness benefit to polygyny is offset by the reduction in relatedness to wives' offspring, such that monogamy is stable for all values of δ_{m}; condition **b** in Table 2.2; Figure 2.2b).

Figure A.1 in Section A.2 shows that these results hold for values of $p_{\mathrm{H}} < 1$. Here $p_{\mathrm{H}} = 0.5$, which is likely an extremely low value of p_{H}: men would attain on average as much reproductive success by other men's wives as by their own in a society



(a) With monogamous females who always provide "high" paternity



(b) With "astute" monogamous females

Figure 2.2: Stability of "suspicious" monogamous males against mutant males with $w_P = 2$, $w_P = 4$, or $w_P = 8$, for $p_H = 1$; w_P denotes the number of wives for polygynous males, and p_H the paternity level of males with females who always provide "high" paternity and of monogamous males with "astute" females. δ_m represents the relative male contribution to the resources transferred to the offspring generation; z describes the relationship between resources and individual fitness; p_L represents the paternity level of polygynous males with "astute" females. See Sections A.1 and A.2 for details. In (a) social monogamy is stable in the darker area, where all conditions are met; **a** is the condition for stability against monogamous males who transfer diagonally, **b** against polygynous males who transfer vertically, **c** against polygynous males who transfer diagonally (Table 2.2). In (b) social monogamy is stable throughout the volume shown.

with a paternity level of $p < 0.5$ (Hartung 1981). For comparison, in contemporary populations men are the biological fathers of their putative children, on average, in 98.3% of cases if they have high confidence of paternity, and in 70.2% of cases if they have low confidence of paternity; actual paternity levels must fall between these values for most societies (Anderson 2006). Assuming that comparable paternity levels characterized our species' recent evolutionary past, this suggests that social monogamy represented a stable outcome in the evolution of human social systems.

2.4 Discussion

These findings show that inclusive fitness theory can account for the evolution of monogamous marriage, and for variation in marriage strategies across societies more generally. Where resources are linked to fitness and are transferred across generations, social monogamy may be a stable evolutionary outcome (i) if dividing resources among the offspring of multiple wives causes a depletion of their fitness value and/or (ii) if females grant husbands higher fidelity in exchange for exclusive investment of resources in their offspring. In both cases, the benefit to monogamy increases as the relative contribution of resources by females decreases.

The historical and ethnographic evidence suggest that these mechanisms likely operated in shaping the evolution of human social systems. In the Old World, polygyny prevails among African societies with subsistence economies based on pastoralism or extensive agriculture (Goody 1976). The relationship between resources and fitness documented for the Gabbra pastoralists of Kenya (Mace 1996) and for the Chewa horticulturalists of Malawi (Holden et al. 2003) indicates that in pastoralism and horticulture the fitness value of resources is not depleted through division. Among the Gabbra, for example, parents provide on average ten camels to marry off a son: three as bridewealth to the bride's kin, and seven to the groom for starting an independent household (Mace 1996). If the division of resources depleted their fitness value, the reproductive success of men owning five camels would be less than half the reproductive success of men owning ten. Conversely, men with five camels have more than half the reproductive success of men with ten (Mace 1996). This is likely because in both subsistence systems productivity is constrained more by availability of labour than by ownership of the primary productive resources (Goody 1976): in

pastoralist societies holdings of livestock can easily be increased through husbandry; in horticultural societies the low productivity afforded by extensive agricultural techniques means that land is rarely a scarce resource (Goody 1976; Gray 1964).

This is in stark contrast with the intensive agriculture practised in the historical societies of Eurasia, where irrigation and ploughing led to increased productivity, which in turn sustained continued population growth. Combined, increased productivity and population growth caused shortages of land. As land scarcity increased, so did the pressure to keep holdings above the minimum size required to set up a viable productive and reproductive unit (Goody 1976; Hrdy and Judge 1993; Section 3.1.2). Under these conditions of habitat saturation, the partitioning of estates depleted their value; in extreme cases the reduction in value was so great that parents commonly designated a single heir, at the expense of all other offspring, through systems of unigeniture (Hrdy and Judge 1993; e.g. Boone 1986, 1988; Voland and Dunbar 1995).[1]

Consistent with our finding that social monogamy can be advantageous where the value of resources is depleted through division, marriage was typically monogamous in

[1]Fraternal polyandry, in which a set of brothers marry a single wife, can also be viewed as a mechanism for reducing the number of heirs to an estate by limiting the number of wives whose offspring have claims to the estate (Goody 1976, p. 17; Goody 1990, Chapter 5). It likely serves this purpose, as an extreme form of unigeniture, in the harsh highland desert environments of Tibet (e.g. Crook and Crook 1988; see review and discussion in Barrett et al. 2002, pp. 224–233). As in the extensive agricultural societies of sub-Saharan Africa, here the land requires high labour input and yields low productivity; as in the other intensive agricultural societies of Eurasia, the risk of land shortages is however high (in this case through low carrying capacity rather than through increased productivity and population growth). This combination of ecological conditions may explain why Tibetan societies resort to polyandry rather than to monogamy.

Polyandry is not a stable outcome of the model developed here; however, fraternal polyandry is not an option in the current setup, since individuals have only one sibling of the opposite sex (Section 2.2). Extension of the model to include fraternal co-husbands may make polyandry a stable outcome, by increasing the payoff of this strategy to males. Interestingly, however, polygyny is generally allowed alongside polyandry, both in Tibetan societies (e.g. Levine and Silk 1997) and elsewhere (e.g. Rivers 1906, for the Todas of South India), although it tends to occur in a small minority of cases; polygynandry is a stable outcome even in the current setup. Theoretical analysis of this type is likely to play a key role in clarifying the ultimate determinants of polyandrous marriage (e.g. Hughes 1982; Smith 1998), while analysis of individual societies may clarify the proximate mechanisms involved (e.g. Levine and Silk 1997). By contrast, the inclusion of polyandrous societies in cross-cultural analyses is problematic (e.g. Section 3.2.1.1), because this strategy is exceedingly rare: only 2 (1.1%) of the 186 societies in the *SCCS* and 7 (0.6%) of the 1267 societies in the *EA* are scored as polyandrous (Gray 1999; White et al. n.d.). Investigation of samples including societies from a specific geographic region or linguistic sub-group is likely to be more fruitful in this context than analyses of worldwide samples.

the agrarian societies of Eurasia with economies based on intensive agriculture (Goody 1976). In line with our expectations, the relative contribution of women to production is lower in these societies compared to other subsistence systems (Goody 1976; Murdock and Provost 1973). Indeed, across societies access to new land for expansion is a key ecological determinant of polygyny (White and Burton 1988), and within societies the incidence of polygyny declines with increasing scarcity of land (White 1988). This raises the possibility that restrictions on polygynous marriage emerged in the ancient societies of Eurasia following the adoption of intensive agriculture, as ownership of land became increasingly critical to economic success, and growing shortages of land imposed greater costs on partibility. Cultural norms promoting high paternity, such as ideologies of honour, virginity, and sexual fidelity, were common in these societies (Mair 1971; Scheidel 2009). To the extent that these norms resulted in an increase in average relatedness between a man and his wife's offspring, our findings suggest that they may have facilitated the establishment of social monogamy in this region.

Of course, any model can capture but a small fraction of variation in human social systems, and must overlook the many historical contingencies, such as the diffusion of religious beliefs (e.g. Goody 1983; Section 3.1.2), that may have influenced their development. Yet placing this variation within an inclusive fitness framework allows us to conceptualize general evolutionary mechanisms shaping the organization of human societies. This finally resolves the crux of anthropological discussions about whether the primary function of marriage is "economic and productive" or "sexual and reproductive" (Goody 1973, p. 189). In evolutionary terms, the proximate economic determinants of marriage underlie its ultimate reproductive function.

Chapter 3

Log-linear analysis of marriage and transfer strategies in the *Standard Cross-Cultural Sample*

3.1 Introduction

3.1.1 Background

If marriage strategies evolved to maximize the effect of inherited resources on inclusive fitness, they will vary with transfer strategies, which determine how resources are passed down the generations. On the model in Chapter 2, monogamy may be advantageous over polygyny because, by definition, it concentrates resources in a limited number of heirs, and/or because females may grant higher fidelity to husbands who invest exclusively in their offspring. In any case, monogamous marriage is only stable if men transfer resources vertically, that is, to their wife's offspring.[1]

In this chapter I use cross-cultural data to test the predicted association between monogamous marriage and the vertical transfer of a man's property, as reflected in social norms regulating marriage and inheritance.

[1]By contrast, the polygamous equilibria generated by the model (not shown) indicate that polygynous and polygynandrous marriage can also be stable if men transfer resources diagonally, that is, to their sister's offspring. As discussed in Section 2.4, polyandrous marriage is never stable in the current setup.

3.1.2 Related research

To my knowledge, Goody's (1976) argument represents the only attempt to formally link monogamous marriage to an emphasis on the transfer of property to lineal heirs. The argument focuses on what Goody (1976) terms "diverging devolution", that is, the transfer of parental property to both sons and daughters, in the form of inheritance or dowry. Diverging devolution is contrasted with systems of "homogenous inheritance", where property is transferred only "homogeneously", that is, between individuals of the same sex; typically, the property of a sonless man is inherited by his collateral male kin rather than by his daughters. Diverging devolution prevails in Eurasia, while homogenous inheritance is practically universal in sub-Saharan Africa.

Central to Goody's (1976) argument is the notion that the higher productivity and consequent population expansion that accompanied the development of intensive agriculture in Eurasia led to scarcity of land in the region; this generated a tendency to retain control of scarce productive resources "within the basic productive and reproductive unit, which in the large majority of cases is the nuclear family" (Goody 1976, p. 20), by favouring children as heirs at the expense of collateral kin. In this context, the provision of daughters with property served as a mechanism to preserve their status, by securing them access to husbands of appropriate standing. In turn, husbands were typically required to match the wife's resources, leading to the establishment of a "conjugal fund" in which the spouses and their children enjoyed rights. Polygynous marriage (but not polygynous mating, e.g. through concubinage) becomes problematic where husbands and wives pool property in this way: for the purpose of inheritance, for example, a man would need to differentiate between his offspring based on the amount of resources their mothers contributed at marriage. Consequently, conjugal community of property is rare among the polygynous, homogenous inheritance societies of sub-Saharan Africa. According to Goody (1976, p. 90) this explains why "the major Eurasian societies have definite tendencies towards monogamy."

Goody (1976) found evidence of association between diverging devolution and monogamous marriage in the *EA*. Further analyses found evidence that advanced agriculture and stratification are causally linked to diverging devolution, which is in turn causally linked to the occurrence of father's brother's daughter marriage, endogamy, the prohibition of premarital sex, and monogamous marriage. To asses the validity of

these inferences in the face of Galton's problem (Section 1.2.3), the analyses had been replicated on several sub-samples of the *EA*, including the *SCCS*, yielding qualitatively similar results (Goody 1976, p. 27; e.g. Buckley and Goody 1974; Goody et al. 1971).

Goody (1976, p. 143) recognized Christianization as a potential confounder, but did not explicitly assess its effect on these inferences. In fact, he never questioned their validity despite discussing at length, in later historical work (Goody 1983, 2000), the role of Christianization on "the development of the family and marriage in Europe" — to use the title of his 1983 book on the topic. This work centres around the notion that the maintenance of the Christian Church as an institution required ownership of property. Thus, following the establishment of the Church in the fourth century CE, marked by the conversion of Emperor Constantine in 312 and the subsequent Christianization of the Roman Empire, the ecclesiastical hierarchies initiated a series of changes in kinship and marriage systems aimed at restricting the range of legitimate heirs, and ultimately at diverting property away from kin groups and into the Church. Some of these changes, like the prohibition of divorce and of remarriage, counteracted the strategies that diverging devolution societies typically use to compensate for the absence of lineal heirs; others, including the promotion of monogamous marriage and the emphasis on children as heirs to the exclusion of collateral kin, simply extended the conjugal focus characteristic of these societies.

Thus, the evidence for association between monogamous marriage and an emphasis on the transfer of property to lineal heirs may reflect a functional relationship, as proposed by Goody (1976), or it may be contingent upon the interference of the Church in the kinship and marriage systems of European societies, as proposed by Goody (1983). In any case, the significance of this evidence for the present analysis is unclear, because vertical transfer as defined in Chapter 2 subsumes diverging devolution as well as inheritance by sons to the exclusion of daughters; the latter falls under homogenous inheritance in Goody's (1976) categorization.

3.1.3 Rationale and objective

The theoretical analysis in Chapter 2 predicts an association between monogamous marriage and the vertical transfer of property. Previous cross-cultural analyses found evidence of association between monogamous marriage and an emphasis on the transfer

of property to lineal heirs, but failed to control for the potentially confounding effect of Christianization on the distribution of marriage and transfer strategies.

Here I test the predicted association using data on marriage and transfer strategies for societies in the *SCCS*, including information on religious affiliation to control for the potentially confounding effect of Christianization. As discussed in Section 1.2.3.1, the *SCCS* is a sample of 186 societies that is broadly representative of human cultural variation in time and space, and minimizes the effects of descent and contact on the distribution of cultural practices.

3.2 Data and methods

3.2.1 Cross-cultural data

The *SCCS* is distributed in electronic form through the *World Cultures* journal website (`http://worldcultures.org/`); I used version `SCCSvar1-2008Map.sav` of the database, obtained on 31 August 2007. Variable identifiers in Sections 3.2.1.1 to 3.2.1.3 follow White et al.'s (n.d.) *SCCS* codebook. All variables used were recoded into binary form, because the number of cases required for the statistical analysis increases rapidly with number of levels per variable (Section 3.2.2). The data in binary form and maps of their geographical distribution are in Section B.1.

3.2.1.1 Marriage strategy

I coded societies as practising monogamous or polygynous marriage based on *SCCS* variable 79. This variable scores societies on the social composition of the prevailing form of family organization, defining monogamy in terms of the prohibition or disapproval of polygyny (Murdock and Wilson 1972). The information is pinpointed in time and space to the focal *SCCS* communities (Section 1.2.3.1).

I excluded the two polyandrous societies and collapsed the two categories for polygynous marriage (limited polygyny, i.e. less than 20% of males having plural wives, and general polygyny, i.e. more than 20% of males having plural wives). This produced a sample with 31 (16.8%) of 184 societies coded as monogamous and 153 (83.2%) coded as polygynous (Table B.1 and Figure B.1b).

3.2.1.2 Transfer strategy

The *SCCS* scores societies separately on the norms regulating the disposition of a man's property in land and of his other goods such as livestock, tools and other artefacts, accumulated food stores, and money (respectively "real" and "movable" property, variables 278 and 279; after Murdock 1963a). These variables were originally coded for the corresponding societies in the *EA* (White et al. n.d.); the available sources do not state whether or in which cases the information refers to the focal communities in the *SCCS*, i.e. whether it is pinpointed to these communities in time and/or space (Section 1.2.3.1).

I included both variables in the analysis, because different inheritance rules may prevail for different types of property (Lowie 1920, p. 255; Murdock 1949, p. 38). For each type of property I coded societies for the presence or absence of norms resulting in vertical transfer, as defined in Section 2.2. The "presence" category subsumed all cases in which the inheritance rules stipulate a man's wife's offspring as his primary heir (including cases where other patrilineal relatives take precedence over wife's offspring). The "absence" category subsumed all cases in which the inheritance rules stipulate a man's sister's offspring as his primary heir (including cases where other matrilineal relatives take precedence over sister's offspring), and cases in which men do not hold individual rights in the type of property in question or in which no rules regulate the transfer of such rights. Where other relatives, typically younger brothers, take precedence over wife's or sister's offspring, property reverts to wife's or sister's offspring when there are no surviving individuals in the designated category of kin (Murdock 1949, p. 37). Because absence of rights and absence of rules are conflated in a single category in the *SCCS* variables, it was not possible to exclude from the analysis societies in which men do not hold individual rights in property; this would have been preferable for the purpose of testing the predicted association, since the model in Chapter 2 focuses on variation in marriage and transfer strategies across societies with intergenerational transfer of resources (Section 2.2).

Based on this coding, norms stipulating the vertical transfer of land were present in 83 (53.5%) of 155 societies and absent in 72 (46.5%) (Table B.1 and Figure B.1c); norms stipulating the vertical transfer of movables were present in 117 (77.0%) of 152 societies and absent in 35 (23.0%) (Table B.1 and Figure B.1d).

Table 3.1: Derivation of binary coding for religious affiliation

Variable 2002*	Variable 713†			
	–	Classical	Mixture	Preclassical
–	–	–	–	Other
Christianized	Christianized	Christianized	Christianized	–
Other	Other	Other	Other	–

* Dichotomized (Section 3.2.1.3). The dash indicates missing data.

† "Classical" represents classical religions; "mixture", mixture of classical and preclassical religions; "preclassical", preclassical religions (Section 3.2.1.3). The dash indicates missing data.

3.2.1.3 Religious affiliation

I coded societies for the presence or absence of Christianization by combining the two *SCCS* variables that provide information on religious affiliation. Variable 713, originally in Whyte (1978b), scores the odd-numbered societies in the *SCCS* as practising a classical or preclassical religion, or a mixture of the two; the classical religions are Buddhism, Christianity, Hinduism, and Islam. The information in this variable is pinpointed in time and space to the focal *SCCS* communities (Section 1.2.3.1), with the exception of two societies (Whyte 1978a); the latter two were not included in the analysis because they lacked data on one or more of the other variables (Section 3.2.2). Variable 2002, based on Korotayev (2003, 2004), specifies the affiliation of societies practising one of the classical religions. The information in this variable is pinpointed to the focal *SCCS* communities in approximately 50% of cases (A. Korotayev, pers. comm., 13 May 2008; Section 1.2.3.1).

To resolve discrepancies between the codings, I dichotomized variable 2002 and combined it with variable 713 as per Table 3.1. This produced a sample with Christianization present in 26 (24.1%) of 108 societies and absent in 82 (75.9%) (Table B.1 and Figure B.1e).

3.2.2 Statistical analysis

I inferred the multivariate pattern of association among marriage strategy, the two transfer strategies, and religious affiliation across societies in the *SCCS* through

hierarchical log-linear analysis. Log-linear analysis is a technique used to model cell counts in contingency tables of a set of two or more categorical variables, with the aim to produce the simplest possible model that can accurately predict the observed cell counts (Agresti 2007, Chapter 7; Tabachnick and Fidell 2007, Chapter 16). This model corresponds to the simplest possible set of associations among levels of the variables that yields cell counts not significantly different from the observed ones.

In the hierarchical implementation of log-linear analysis, the final model is obtained by initially constructing a "saturated" model, which includes terms capturing all of the possible interactions among the variables: the expected cell counts produced under this model perfectly match the observed data. Successively, these terms are removed one at the time through a process of hierarchical backward elimination, starting from the highest-order interaction. After each removal, a goodness-of-fit test evaluates the fit between the expected cell counts produced under the simpler model and the observed data: if expected and observed counts differ significantly, the eliminated effect is retained for inclusion in the final model. This process is repeated until no further terms can be removed without significantly worsening the fit of expected and observed cell counts.

The optimal model is evaluated in terms of the overall fit of expected and observed cell counts, as measured by a goodness-of-fit statistic such as the likelihood ratio χ^2, and in terms of cell-by-cell fit, as measured by standardized residuals. "Good" models have non-significant values of the goodness-of-fit statistic, indicating that the expected cell counts they generate are not significantly different from the observed counts. Standardized residuals provide an indication of the deviation between expected and observed counts for each cell, with values in excess of ± 1.96 indicating poor fit.

I performed the analysis using the SPSS HILOGLINEAR and SPSS LOGLINEAR programmes (SPSS Inc. 2006), following the procedure described in Tabachnick and Fidell (2007, pp. 890–908).

3.3 Results

The usable sample for the log-linear analysis consisted of 87 societies with data on all four variables (Table 3.2); all of the 24 cells in the six two-way contingency tables for this sample had expected frequencies greater than one, while three (12.5%) had expected

Table 3.2: Cross-tabulation of the variables for the 87 cases included in the log-linear analysis*

Marriage	Land	Movables	Religion	
			Christianized	Other
Monogamous	Vertical	Vertical	8	10
		Other	0	0
	Other	Vertical	0	1
		Other	1	0
Polygynous	Vertical	Vertical	6	30
		Other	0	1
	Other	Vertical	3	15
		Other	3	9

* "Marriage" represents the marriage strategy; "land", the transfer strategy for land; "movables", the transfer strategy for movables; "religion", the religious affiliation.

frequencies smaller than five. A minimum sample of $5 \cdot 2^4 = 80$ is recommended with four binary variables; up to 20% of cells with expected frequencies smaller than five is acceptable (Tabachnick and Fidell 2007, pp. 861–862).

As shown in Table 3.3a, the hierarchical log-linear procedure identified a model that included all four first-order effects (transfer strategy for movables, marriage strategy, religious affiliation, transfer strategy for land) and three of the six possible two-way associations (the interaction between transfer strategies for the two types of property, the interaction between marriage strategy and transfer strategy for land, the interaction between marriage strategy and religious affiliation). The model had a likelihood ratio $\chi^2(8) = 4.50$ with 95% confidence limits from 0.00 to 6.52, $p = 0.81$, indicating a good fit between the observed frequencies and the expected frequencies generated by the model. Accordingly, the standardized cell residuals ranged from -0.73 to 1.05, indicating that none of the 16 cells in the classification table produced by the model was an outlier.

Inclusion of the four one-way effects in the model means that, for each variable, the distribution of cases across the two levels was skewed (Spicer 2005, p. 209). The standardized parameter estimates in Table 3.3b provide an indication of the relative strength of the effects in predicting cell frequencies. Of the 87 societies in the sample (Table 3.2), 73 (83.9%) presented norms stipulating the vertical transfer of movables,

Table 3.3: Summary of the hierarchical log-linear model

(a) Significance tests (partial likelihood ratio χ^2) and 95% confidence intervals

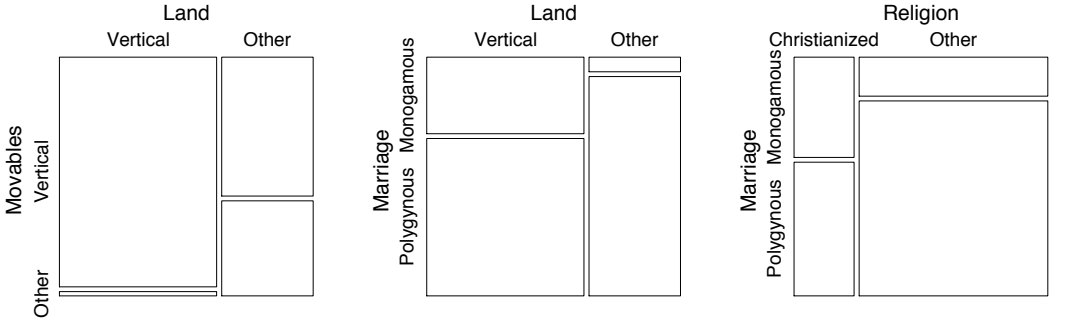
Effect*		$\chi^2(1)$	95% CI	p-value
First-order	Movables	43.84	21.73–73.64	< 0.001
	Marriage	26.80	10.35–50.93	< 0.001
	Religion	24.44	8.90–47.66	< 0.001
	Land	6.15	0.24–19.72	0.013
Second-order	Movables by land	20.49	6.58–42.08	< 0.001
	Marriage by land	5.94	0.20–19.33	0.015
	Marriage by religion	5.77	0.16–19.03	0.016

(b) Raw (λ) and standardized (λ/SE) log-linear parameter estimates

Effect*†		λ	λ/SE
First-order	Movables	−1.09	−4.08
	Marriage	0.73	3.58
	Religion	0.43	3.13
	Land	0.05	0.16
Second-order	Movables by land	0.90	3.37
	Marriage by land	0.50	2.53
	Marriage by religion	0.33	2.40

* "Marriage" represents the marriage strategy; "land", the transfer strategy for land; "movables", the transfer strategy for movables; "religion", the religious affiliation.

† Each effect is summarized by a single parameter value, with one level of a variable taking the positive value of the parameter and the other taking the negative value.



(a) Movables by land **(b)** Marriage by land **(c)** Marriage by religion

Figure 3.1: Mosaic plots of the two-way interactions included in the hierarchical log-linear model. The area of each cell in a plot is proportional to the number of observations in the cell. "Marriage" represents the marriage strategy; "land", the transfer strategy for land; "movables", the transfer strategy for movables; "religion", the religious affiliation.

67 (77.0%) practised polygyny, 66 (75.9%) were not Christianized, and 55 (63.2%) presented norms stipulating the vertical transfer of land.

The three two-way effects included in the model indicate that marriage strategy and transfer strategy for land were associated with each other and, respectively, with religious affiliation and with transfer strategy for movables, and that these effects were not confounded (Spicer 2005, p. 209). The standardized parameter estimates in Table 3.3b show that the interaction between the transfer strategies for the two types of property was the strongest predictor of cell frequencies, while the other two effects were of comparable magnitude.

The direction of the two-way effects included in the model is illustrated by the mosaic plots in Figure 3.1. Norms stipulating the vertical transfer of land were present in 54 (74.0%) of 73 societies with analogous norms for the transfer of movables, compared to 1 (7.1%) of 14 societies lacking such norms for movables (Table 3.2 and Figure 3.1a). Norms stipulating the vertical transfer of land were present in 18 (90.0%) of 20 monogamous societies, compared to 37 (55.2%) of 67 polygynous societies (Table 3.2 and Figure 3.1b). Christianization was present in 9 (45.0%) of 20 monogamous societies, compared to 12 (17.9%) of 67 polygynous societies (Table 3.2 and Figure 3.1c).

3.4 Discussion

The log-linear analysis of marriage strategy, transfer strategies for land and movables, and religious affiliation across societies in the *SCCS* shows that norms stipulating the vertical transfer of land exist in a significantly larger proportion of monogamous societies, compared to polygynous societies. This is consistent with the association between monogamous marriage and the vertical transfer of property predicted by the theoretical analysis in Chapter 2. Additionally, the log-linear analysis shows that norms stipulating the vertical transfer of land exist in a significantly larger proportion of societies with analogous norms for the transfer of movables, compared to societies without such norms. However, despite the convergence of transfer strategies for the two types of property, there is no association between marriage strategy and transfer strategy for movables. Together, these findings suggest that monogamous societies tend to *specifically* regulate the vertical transfer of land. This bolsters the interpretation of anthropological observations on the distribution of marriage strategies provided in Section 2.4: historically, the emergence and prevalence of monogamous marriage among the land-based societies of Eurasia were driven by the depletion in value resulting from the partitioning of estates among multiple heirs. As noted in Section 2.4, availability of land is a key correlate of polygynous marriage, both within and across societies (White 1988; White and Burton 1988).

Finally, the log-linear analysis shows that Christianization is present in a significantly larger proportion of monogamous societies, compared to polygynous societies. This finding supports explanations of the distribution of marriage strategies that posit an association between monogamy and Christianization (e.g. Goody 1983). At the same time, however, it challenges those explanations that avoid discussing the origin and occurrence of this marriage strategy by dismissing it as a by-product of Christianization.[1] The inferred pattern of association strongly diverges from the pattern expected if monogamous marriage were explained away by Christianization.

[1]For example, under the heading *The conjugal union*, Zonabend (1996, p. 56) refers only in passing to monogamous marriage, and even then indirectly, arguing that "Western societies are familiar with polygyny, though they do not approve of it (the Christian Church was very quick to condemn it as a sign of paganism)"; in the remainder of the section, which extends over four and a half pages, he details various ethnographic examples of polygynous and polyandrous marriage.

Consistently, the historical and ethnographic evidence conflict with the "cultural infection" scenario implicit in explanations that view monogamy as a by-product of Christianization (Section 1.2.3.2), whereby societies "passively" adopt monogamous marriage alongside Christianity. As noted in Section 2.1, restrictions on polygynous marriage are recorded in the earliest historical documents, and monogamous marriage was established in ancient Greece and Rome prior to Christianization. The Christian Church formally opposed polygynous marriage only since at least 600 CE, possibly incorporating the Roman custom into its doctrine (Cairncross 1974, pp. ix, 221). Further, the Church's attempts to eradicate polygyny were typically met with resistance (Cairncross 1974, pp. 60–61). In sub-Saharan Africa for example, where Christian missionary efforts began as early as in the fifteenth century, the prescription of monogamous marriage clashed with the deeply rooted polygynous aspirations of local leaders, and of the male population in general (Harries 1953, pp. 336–337). Possibly to counteract the spread of Islam in the region, driven by its compatibility with polygyny, *de facto* plural marriage has been tolerated among African Christians, and in some cases openly sanctioned (Cairncross 1974, pp. 213–214). Incidentally, an analogous situation may account for the co-occurrence of polygyny and Christianization in some of the *SCCS* societies included in the analysis.

Elsewhere, the adoption of monogamous marriage was likely mediated by changes in other aspects of social organization that accompanied the spread of the Christianity. Among the native Mexican and Andean populations, for example, polygynous marriage had been the exclusive prerogative of the élites in pre-colonial times. With the introduction of monogamous marriage by the Church following the Spanish conquest in the sixteenth century, these groups typically replaced polygyny with concubinage; "Christian marriage" was largely established in Mexico and in Peru by the end of the century (Bernand and Gruzinski 1996, pp. 164, 176–181). Interestingly, however, the Church's imposition of monogamous marriage coincided with introduction by the Spanish Crown of private property and will-making (Bernand and Gruzinski 1996, pp. 172–173). Thus it is possible that changes in the control and transfer of property facilitated the establishment of monogamous marriage in these groups.

On this evidence, "cultural infection" explanations for the distribution of monogamous marriage seem too simplistic. In the African case the relative rates of spread across societies of Christianity and Islam appear to have been affected by the societies'

marriage strategy, rather than vice versa; in the American case, the acquisition of monogamous marriage was likely mediated by changes in other aspects of social organization that accompanied the spread of Christianity. Rather, the evidence suggests a more interesting question: historically, why have some societies resisted monogamous marriage, while others appear to have readily adopted it? The anthropological observations discussed in Section 2.4 indicate that the distribution of marriage strategies reflects property considerations, which in turn reflect ecological determinants. For example, the deeply rooted polygynous aspirations of sub-Saharan African men may reflect the benefits afforded by polygynous marriage in horticultural and pastoralist societies, and this may explain the resistance to monogamous marriage encountered by Christian missionaries in the region.

On the model developed in Chapter 2, property considerations of this type represent the proximate pathways through which the ultimate function of marriage is effected (Section 1.2.2); the concern of parents with preservation of the status of their children discussed by Goody (1976) provides a candidate psychological mechanism (although in Goody's framework the preservation of status is viewed as the ultimate cause of monogamous marriage, e.g. Goody 1969; Section 3.1.2). The analysis presented in this chapter supports a corollary prediction of the model, but the evidence is to be taken as suggestive. Potential confounders include the error introduced by Galton's problem — as discussed in Section 1.2.3.1, use of the *SCCS* minimizes, but does not control for, the effects of descent and contact on the distribution of cultural practices — and the error introduced by the use of data not pinpointed in time and/or space to the focal *SCCS* communities (Section 3.2.1), which may account, for example, for the co-occurrence of polygyny and Christianization in some entries in the sample. A conclusive test of the model will come from investigation of the archaeological and historical sources documenting the emergence of monogamous marriage (Section 2.1), and from investigation of the historical and ethnographic evidence describing transitions between marriage strategies (e.g. the recent shift from polygyny to monogamy in several Muslim countries, or the shift from monogamy to polygyny among the Mormons during the nineteenth century; Cairncross 1974, p. 222). Importantly, the analyses presented in the previous and present chapters provide a robust theoretical framework to guide and focus these investigations.

Chapter 4

Reconstructing the history of marriage strategies in Indo-European-speaking societies

4.1 Introduction

4.1.1 Background

Explanations for monogamous marriage have centred around the prevalence of this practice in Eurasia (Holy 1996, pp. 62–63), linking its emergence to the development of idiosyncratic features of societies in the region. These include, for example, the establishment of large nation states (e.g. Alexander 1987; Section 2.1) and democracy (e.g. Fox 1997), the spread of Christianity (e.g. Goody 1983, 2000; Section 3.4), the onset of industrialization and urbanization (e.g. Betzig 1982, 1986; van den Berghe and Barash 1977) and of economic development more generally (e.g. Gould et al. 2008). Consistently, cross-cultural analyses show that societies scoring high on scales measuring "societal complexity" tend towards monogamous marriage (Levinson and Malone 1980, p. 37; e.g. Blumberg and Winch 1972; Lee 1979; McNett 1973; Osmond 1965, 1969; Sheils 1971).

By focusing on the cross-cultural distribution of marriage strategies, these studies fail to account for their history. As discussed in Sections 2.1 and 3.4, restrictions on polygynous marriage appear in the earliest historical records, long predating the development of aspects of social organization typically associated with Eurasian

societies, and with "societal complexity" and "modernization" more generally. In this chapter I reconstruct the pattern of change in marriage strategies in the history of societies speaking IE languages, using cross-cultural data in the systematic and explicitly historical framework afforded by the phylogenetic comparative approach (Section 1.2.3.2).

As discussed in Section 1.2.3.2, phylogenetic tree-building analyses of linguistic data support Renfrew's (1987) hypothesis for the origin of the IE language family, which envisages an expansion from Anatolia with the spread of agriculture starting between 7000 and 6000 BCE. This scenario involves an early split of IE languages from their sister group, the extinct Anatolian family, which comprises the extinct languages Hittite, Palaic, Lydian, Luwian, and Lycian; together, IE and Anatolian form the Indo-Hittite language family (Ruhlen 1991, pp. 325–327). Consistent with this scenario, I use the term "Proto-Indo-European" (PIE) for the hypothetical ancestor of IE languages and "Proto-Indo-Hittite" (PIH) for the hypothetical ancestor of Indo-Hittite languages, and for the hypothetical "proto-societies" that spoke them. Other classifications, based on alternative explanations for the origin of the IE language family, use PIE for the ancestor of IE and Anatolian languages (i.e. they classify Anatolian languages as IE; e.g. Mallory and Adams 2006). To avoid confusion, in this chapter and in Chapters 5 and 6 I have changed instances of the latter usage to the one stated here.

4.1.2 Related research

Early IE marriage strategies have been reconstructed on the basis of linguistic and ethnographic evidence. The linguistic evidence is, at best, tenuous. The correspondence of the Middle Irish (Celtic sub-group, *c.* 900–1200 CE) and Avestan (Iranian sub-group, first millennium BCE) terms for "concubine, wanton woman" suggests that PIH society recognized some form of polygynous mating, if not polygynous marriage; this interpretation is supported by the use of specialized terms to designate legitimate children (Huld and Mallory 1997, p. 123). A second line of evidence relates to the concept of widowhood: while it is possible to reconstruct a PIH term for "widow", there is no corresponding term for "widower". One interpretation of this pattern is that male widowhood was not recognized in PIH society because men married polygynously, such that the death of one wife did not affect their marital status (Huld 1997, p. 642). Implicit in this interpretation are however a number of unrealistic assumptions, for

example that *all* PIH men married multiple wives and that they rarely, if ever, outlived their wives; both represent demographic impossibilities.

Based on the ethnographic evidence, Murdock (1949, p. 349) reconstructed "an Eskimo type of social structure in the prehistory of the Indo-European peoples." The defining features of this type of social organization are the presence of the Eskimo system of cousin terminology and the absence of exogamous unilineal kin groups; additional typical characteristics include the presence of monogamy, independent nuclear families, and neolocality, but variant sub-types characterized by non-neolocal marital residence may feature polygyny and extended families (Murdock 1949, p. 227).[1] The reconstruction was inferred from the social organization of five societies speaking IE languages, representing four of the major sub-groups of the language family. Specifically, the social systems of Yankees (Germanic sub-group) and Ruthenians (Slavic sub-group) are of the Eskimo type, the social systems of Albanians (Albanian sub-group) and Ossets (Indo-Iranian sub-group) include features suggesting "Eskimo antecedents", while the social system of the Kurds (Indo-Iranian sub-group) is not incompatible with the Eskimo type. Quite apart from the small number of societies upon which the reconstruction was based, Murdock's (1949) approach presents a serious methodological issue. According to Fox (1967, p. 262), modern IE terminologies for kin and affines (in-laws) tend to show a much stronger bias towards the nuclear family than was the case for early IE terminological systems. This brings into question the validity of inferences about past social organization drawn from kinship and affinal terminologies (see Section 5.1.2).

Finally, Fortunato and Mace (2009) used the ethnographic evidence in a phylogenetic comparative framework, to test the hypothesis of co-evolution of bridewealth with polygyny (Hartung 1982) and of dowry with monogamy (Gaulin and Boster 1990) in a sample of 51 societies speaking IE languages. This analysis reconstructed monogamy with dowry as the most likely state at the root of a phylogenetic tree representing the historical relationships among the 51 societies; in addition, the tree included Hittite, thus the root of the tree corresponded to PIH (Sections 4.1.1 and 4.2.2). The

[1] In the Eskimo type of cousin terminology all cousins are equated with each other but differentiated from siblings. Unilineality refers to kin groups organized around principles of matri- or patrilineal descent. Neolocality indicates residence of married couples apart from the kin of either spouse (Section 5.1.1).

reconstruction was obtained using the maximum-likelihood phylogenetic comparative method developed by Pagel (1994) and implemented in Discrete (Pagel n.d.); this method estimates the evolutionary scenario that is most likely to have produced the observed distribution of states of the two traits across taxa at the tips of the tree. The tree was generated through phylogenetic tree-building analysis of the corresponding 51 speech varieties in Dyen et al.'s (1992) IE basic vocabulary database (Section 4.2.2), using a maximum-parsimony optimality criterion, as implemented in PAUP* 4.0b4a (Swofford 2002); this approach finds the tree or set of trees that optimizes the degree of fit to the data. However, the use of a "best" tree for phylogenetic comparative analysis is problematic, because results are affected by the topology and other parameters (e.g. branch lengths) of the tree used (e.g. Martins and Housworth 2002; Section 1.2.3.2). Thus, while controlling for the effect of descent on the distribution of cultural practices, Fortunato and Mace's (2009) reconstruction may be contingent upon the phylogenetic tree model used to represent how the societies are related.

4.1.3 Rationale and objective

For the most part, previous attempts to infer early IE marriage strategies from linguistic and ethnographic data have failed to use a systematic and explicitly historical approach. Where such an approach has been taken, the available methods did not account for uncertainty in the phylogenetic tree model used to represent population history.

Here I employ a phylogenetic comparative method, in a Bayesian RJ-MCMC framework, to reconstruct the pattern of change in marriage strategies in the history of societies speaking IE languages. As discussed in Section 1.2.3.2, this approach provides information about the degree of statistical uncertainty in estimation of parameters of interest to the comparative question (e.g. in the rates of trait change or in the values of the ancestral states of the trait). The effect of phylogenetic uncertainty is accounted for by estimating parameters over a probability sample of trees; similarly, uncertainty in the model of trait evolution is accounted for by estimating parameters over a probability sample of models. This yields estimates that are not dependent on any specific model of how the taxa are related or of how the trait has evolved.

4.2 Data and methods

I used data on marriage strategy from the *EA* (Gray 1999; Murdock 1967b) for a sample of societies speaking IE languages (Section 4.2.1). The cross-cultural data were mapped onto a sample of trees representing how the societies are related, obtained by Pagel et al. (2007) from tree-building analysis of Dyen et al.'s (1992) IE basic vocabulary database (Section 4.2.2). On the cross-cultural data and tree sample I used the phylogenetic comparative method developed by Pagel and colleagues (Pagel and Meade 2005, 2006; Pagel et al. 2004) to reconstruct ancestral states of marriage strategy (Section 4.2.3).

4.2.1 Cross-cultural data

The *EA* is distributed in electronic form through the *World Cultures* journal. Variable identifiers in this section follow Gray's (1999) *EA* codebook. The data in binary form and maps of their geographical distribution are in Section B.2.

I collated the cross-cultural sample by matching societies scored as speaking IE languages (based on *EA* variable 98) with speech varieties in Dyen et al.'s (1992) IE basic vocabulary database (Section 4.2.2), where needed using information from additional ethnographic and linguistic sources (e.g. Gordon 2005; Levinson 1991–1996; Price 1989; Ruhlen 1991). I also checked for correspondence between speech varieties in the linguistic database and the 62 societies in the *EA* with linguistic affiliation unknown and located in East Eurasia or in the Circum-Mediterranean region (based on *EA* variable 91).

In some cases, more than one speech variety in the linguistic database could be matched with the same society in the *EA*. For example, Dyen et al. (1992) include five entries for Greek: three for dialectal forms (Greek D, Greek K, Greek ML), one for modern Greek (Greek Mod), and one for modern spoken Greek (Greek MD), the latter compiled from dictionary data. In these cases, where available I selected the variety derived from dictionary data, which is likely to be less specific than other entries; alternatively, I selected the variety with data for the greatest number of meanings (Section 4.2.2), or the first variety listed in Dyen et al. (1992, pp. 99–101).

The phylogenetic tree model used to represent how societies are related captures the process of diversification of taxa from a common ancestor; therefore, I included in the sample only societies located in Eurasia, corresponding to the geographic range of

IE languages before 1492 CE (Diamond and Bellwood 2003). I excluded the Icelanders because the *EA* description for this society refers to 1100 CE, while the descriptions for the 27 societies included in the sample refer to the "ethnographic present", with dates ranging from 1880 to 1960 CE, and median 1945 CE (Murdock 1967b).

I coded societies as monogamous (state M) or polygynous (state P) based on *EA* variable 9, which scores societies on the prevailing form of family organization (after Murdock 1962). I collapsed the five categories for polygynous marriage, thus ignoring the distinction between limited and general polygyny (Section 3.2.1.1), between general polygyny with sororal and non-sororal co-wives, and between general polygyny with co-wives occupying the same or distinct dwellings. This produced a sample with 18 (66.7%) of 27 societies coded as monogamous and 9 (33.3%) coded as polygynous (Table B.2 and Figure B.2b).

4.2.2 Tree sample

I used Pagel et al.'s (2007) posterior probability sample of 750 phylogenetic trees to represent how societies in the cross-cultural sample are related by way of descent from a common ancestor. Trees are present in the sample in proportion to their posterior probability, which is the probability of the tree conditional on the data and model of word evolution used in the tree-building analysis, and can be interpreted as the probability that the tree is correct (Huelsenbeck et al. 2001). The consensus tree in Figure 4.1 summarizes the 750 trees in the sample. For example, the Ibero-Romance speech varieties included in the tree-building analysis (Brazilian, Portuguese ST, Spanish, and Catalan) share an ancestor in 84% of the trees in the sample (indicated by the arrow); the probability that they are a "monophyletic" group is thus 0.84, given the data and model of word evolution used in the tree-building analysis. As discussed in Section 4.1.3, use of a tree sample instead of a single "best" tree amounts to incorporating phylogenetic uncertainty in the comparative analysis; the degree of phylogenetic uncertainty at several of the nodes in Figure 4.1 emphasizes the importance of doing so in this case.

Pagel et al. (2007) inferred the posterior probability distribution of trees from Dyen et al.'s (1992) IE basic vocabulary database, using the Bayesian MCMC phylogenetic tree-building method developed by Pagel and Meade (2004). The linguistic database includes word forms and cognacy judgements for 95 modern IE speech varieties

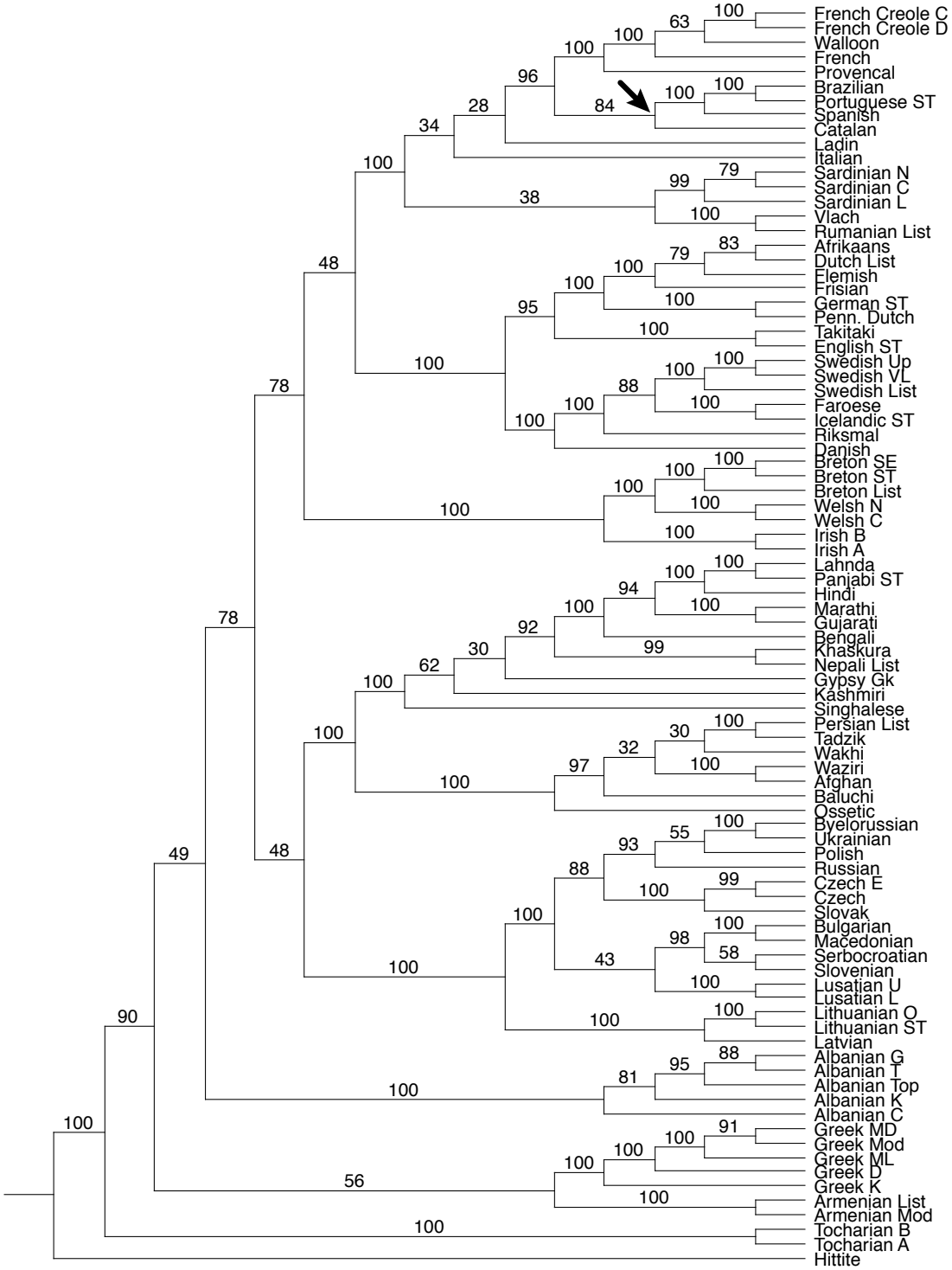


Figure 4.1: Majority-rule consensus tree of Pagel et al.'s (2007) sample of 750 trees for 84 IE speech varieties and three outgroups. The tree includes nodes present in $> 50\%$ of trees in the sample, plus other compatible groupings; the value above each node is the node's posterior probability as a percentage. The arrow marks the ancestor of the Ibero-Romance varieties.

(languages, dialects, and creoles) across the Swadesh 200-word list of items of basic vocabulary; two or more word forms are cognate if they share a common origin. Swadesh lists consist of cross-culturally universal items of vocabulary such as pronouns, body parts, and numerals, which are less prone to innovation and borrowing (i.e. horizontal transmission) than other meanings (Swadesh 1952; Section 1.2.3.2).

The tree-building analysis was performed on a data matrix obtained from the linguistic database as follows. First, Pagel et al. (2007) excluded eleven speech varieties suspected of methodological bias by Dyen et al. (1992), and added data for three extinct varieties (Hittite, Tocharian A, Tocharian B) to be used as "outgroup" taxa. Outgroups provide information on the direction of change in the data by virtue of being distantly related to the groups under investigation, the "ingroup" taxa; they are used in tree-building for determining ancestor-descendant relationships (Felsenstein 2004, p. 6). As noted in Section 4.1.1, Hittite belongs to the extinct sister-group to the IE languages, the Anatolian sub-group; the two known dialects of Tocharian, A and B, are extinct IE speech varieties (Ruhlen 1991, p. 325). Second, Pagel et al. (2007) transformed the linguistic data into a binary matrix, with 87 rows corresponding to the speech varieties and 4049 columns corresponding to classes of cognates; speech varieties were coded for presence or absence of word forms belonging to each cognate class.

I obtained the tree sample from Mark Pagel. I pruned the trees to retain only the speech varieties corresponding to the 27 societies in the cross-cultural sample (Section 4.2.1), plus the outgroup Hittite, using Andrew Meade's programme BayesTrees. I preferred this strategy, over the alternative of generating a tree sample for the speech varieties included in the analysis (e.g. Fortunato et al. 2006), because the accuracy of phylogenetic tree-building grows with increased sampling of taxa (e.g. Zwickl and Hillis 2002). Hittite was retained for consistency with previous work (Fortunato et al. 2006; Fortunato and Mace 2009), but was assigned no marriage strategy data for the purpose of the comparative analysis (Section 4.2.3).

4.2.3 Comparative analysis

Reconstruction of ancestral states using the phylogenetic comparative method developed by Pagel and colleagues (Pagel and Meade 2005, 2006; Pagel et al. 2004) is performed using BayesMultistate, available as part of the BayesTraits package (Pagel and Meade n.d.) from `http://www.evolution.rdg.ac.uk/BayesTraits.html`. Unless

otherwise specified, the information in this section is based on Pagel and Meade (2005, 2006), Pagel et al. (2004), and on the BayesTraits manual (Pagel and Meade n.d.). I describe the method and its application in detail in Appendix C.

Given the cross-cultural data and tree sample, BayesMultistate uses parameters q_{MP} and q_{PM} to describe the evolution of the trait "marriage strategy" on a tree. q_{MP} and q_{PM} measure the instantaneous rates of change respectively from monogamy to polygyny (i.e. from state M to state P) and from polygyny to monogamy (i.e. from state P to state M); they are used to define the probabilities of these changes, the probabilities of the two states at internal nodes on the tree, and the likelihood of the data, which is the probability of the data given the tree and the model of trait evolution specified by the rates (Pagel 1994, 1997, 1999; Section C.1). In the likelihood calculations BayesMultistate treats taxa that are not assigned comparative data, like the outgroup Hittite in this case (Section 4.2.2), as taking any state with equal probability.

In Bayesian RJ-MCMC mode, BayesMultistate uses RJ-MCMC methods to estimate the posterior probability distributions of rate parameters, of ancestral states at internal nodes on a tree, and of the possible models of trait evolution specified by the rate parameters, as described in Sections C.1 and C.2. Four model categories are possible in this case: that q_{MP} and q_{PM} take distinct positive values, that they take the same positive value, or that either one is set to zero while the other takes a positive value. The posterior probability of a parameter value is a quantity proportional to its likelihood of having produced the observed data, and represents the probability of the parameter value given the data and model of trait evolution. Schematically, the posterior probability distributions are estimated by running RJ-MCMC chains that sample states in the model of trait evolution in proportion to their posterior probability, across trees in the tree sample; a state in the model consists of model category, values of the rate parameters, and ancestral state probabilities. Combining estimates over the sample produced by a chain amounts to "averaging" inferences over uncertainty in the phylogeny, in the parameters of the model of trait evolution, and in the model itself (Section 4.1.3).

I performed five sets of analyses, each comprising five separate chains started from random seeds (Section C.3). One set estimated the posterior probability distributions of states M and P at internal nodes on the consensus tree summarizing the tree sample. The means of the posterior probability distributions of states M and P

at a given node, denoted p(M|node) and p(P|node), are multiplied by the posterior probability of the node itself, denoted p(node), to produce the combined probabilities of the two states at the node, denoted p(M) and p(P); p(M|node) + p(P|node) = 1, thus p(M) + p(P) = p(node). This means that if reconstruction of the node itself is uncertain, i.e. if p(node) < 1, the value of p(node) sets an upper limit to the confidence that can be placed in the ancestral state reconstructions for the node. As a rule of thumb, confidence can be placed in reconstructions with combined probabilities ≥ 0.70.

The other four sets of analyses were used to assess explicitly the relative "fit" of states M and P at nodes PIH and PIE. For each node, one set of analyses was run with the node fixed ("fossilized") to state M and one with the node fixed to state P. The posterior probability distributions of $\log_e$(likelihood) values sampled by the chains reflect how well a given fossil state fits the node; a measure called the "Bayes factor", which is used to compare posterior probability distributions (Kass and Raftery 1995; Raftery 1996), provides an indication of the strength of the evidence in favour of one state over the other at the node. The Bayes factor for state M over state P is denoted B_{MP}. $2\log_e(B_{\mathrm{MP}})$ is approximated as twice the difference between $\log_e[H(\text{likelihood})]$ for a chain fixed on state M and $\log_e[H(\text{likelihood})]$ for a chain fixed on state P, where $\log_e[H(\text{likelihood})]$ is the natural logarithm of the harmonic mean of the likelihood values. In theory, values of $2\log_e(B_{\mathrm{MP}}) > 0$ represent evidence for state M and values of $2\log_e(B_{\mathrm{MP}}) < 0$ evidence for state P. Specifically, the evidence for a given state is "weak" for $0 < |2\log_e(B_{\mathrm{MP}})| < 2$, "positive" for $2 < |2\log_e(B_{\mathrm{MP}})| < 5$, "strong" for $5 < |2\log_e(B_{\mathrm{MP}})| < 10$, "very strong" for $|2\log_e(B_{\mathrm{MP}})| > 10$ (Raftery 1996, p. 165). In practice, however, harmonic means of likelihood values may vary across runs: they are expected to converge to the same value if the chains are run to infinity. Consequently, I take the conservative approach recommended by Pagel and Meade (n.d.), which disregards any evidence for either state given by $|2\log_e(B_{\mathrm{MP}})| < 2$.

I determined the RJ-MCMC chain specifications through preliminary maximum-likelihood and MCMC runs, all with nodes not fossilized. These specifications, explained in detail in Section C.3, ensure that the RJ-MCMC chains sample parameter space adequately and ultimately converge to the posterior probability distribution of states in the model of trait evolution. I ran the RJ-MCMC chains for 10^8 iterations, sampling every 10^3, with an additional burn-in of 10^6, and rate deviation set to 50. All chains used a uniform prior on the models and an exponential prior on the rate

parameters; the mean of the exponential prior was seeded from a uniform hyperprior on the interval 0–10. The shape of the prior distribution (exponential or gamma) and the interval of the hyperprior (0–10 or 0–20) only marginally affected the mean of the posterior probability distributions of $\log_e$(likelihood) values and of ancestral states, returning qualitatively similar results.

For each set of analyses, convergence to the posterior probability distribution of states in the model of trait evolution was assessed by comparing the samples returned by the separate chains, through visual inspection of (i) time-series plots of $\log_e$(likelihood) values, (ii) the posterior probability distributions of model categories, and (iii) the average deviation of parameter estimates across runs. The near-independence of sampling events was judged from the autocorrelation of the $\log_e$(likelihood) values of successive states sampled by the chains. In all cases, these diagnostics indicated that the chains sampled the target distributions adequately.

4.3 Results

For each set of analyses, I compared the $\log_e[H(\text{likelihood})]$ values for the states in the model of trait evolution sampled by the separate chains at convergence; I present results for the chain that returned the median value of the $\log_e[H(\text{likelihood})]$.

I discuss the ancestral state estimation at nodes on the consensus tree in Section 4.3.1 and the fossilization of nodes PIH and PIE in Section 4.3.2.

4.3.1 Estimation of ancestral states on the consensus tree

At convergence, the chain sampled states in the model of trait evolution with mean $\log_e$(likelihood) $\pm$ SD $= -11.43 \pm 0.93$ (range: -21.34 to -9.94; auto-correlation coefficient: $r = 0.003$; mean acceptance rate: 22.9%; Section C.3).

I discuss separately the posterior probability distribution of model categories returned by the chain (Section 4.3.1.1) and the ancestral state estimates over all model categories (Section 4.3.1.2).

4.3.1.1 Posterior probability distribution of model categories

The chain sampled the four possible model categories with the frequencies reported in Table 4.1a: for example, q_{MP} and q_{PM} were assigned to the same rate class in 87.8% of

the 10^5 sampled points (model category 1). Over the four model categories, rates were assigned to 1.01 ± 0.08 non-zero classes (mean ± SD; range: 1–2 non-zero classes); this indicates that the evolutionary transitions that produced the observed distribution of states of marriage strategy across societies in the sample can be described by a simple model of trait evolution based on only one non-zero rate class.

Nodes PIH and PIE reconstructed as monogamy with high posterior probabilities under model categories 1, 3, and 4, and as polygyny with $p(\mathrm{P}|\mathrm{node}) = 1$ under model category 2 (Table 4.1b). In the latter category, transitions from monogamy to polygyny are excluded, because q_{MP} is set to zero. This forces nodes PIH and PIE to reconstruct as polygyny: under this category, any variation in states of marriage strategy at the tips of the tree is the result of transitions from polygyny to monogamy. In other words, the presence of polygyny at the tips could not be accounted for if PIH and/or PIE reconstructed as monogamy. However, models in category 2 returned a mean $\log_e$(likelihood) value 1.67 units worse than models in the category that returned the best mean $\log_e$(likelihood) value (category 1, Table 4.1a), and 1.47 units worse than the mean $\log_e$(likelihood) value over the four model categories. This suggests that the evolutionary scenario described by model category 2 ("deep" polygyny; no transitions from monogamy to polygyny) is unlikely to have produced the observed distribution of states of marriage strategy across societies in the sample.

4.3.1.2 Posterior probability distributions of ancestral states

Over the four model categories, nodes PIH and PIE reconstructed as monogamy with high posterior probabilities (Table 4.1b). The posterior probability distribution is more strongly skewed towards high values for state M at node PIE, as reflected in the higher value of $p(\mathrm{M}|\mathrm{node})$ at this node (Figures 4.2 and 4.3).

Monogamy reconstructed with high posterior probabilities through to nodes A and B on the consensus tree summarizing the tree sample, but phylogenetic uncertainty limits the confidence that can be placed in these inferences (Figure 4.4 and Table 4.2). Node D (the common ancestor of societies speaking Italic, Germanic, and Celtic languages) and node F (the common ancestor of societies speaking Baltic and Slavic languages) reconstructed as monogamy with high posterior probabilities. Node E (the common ancestor of societies speaking Indian and Iranian languages) reconstructed as polygyny with high posterior probability.

Table 4.1: Summary of the posterior probability distribution of model categories

(a) Rate classes, frequencies, and $\log_e$(likelihood) values

Model category	Rate class*		Frequency†		$\log_e$(likelihood) (mean ± SD)
	q_{MP}	q_{PM}	Absolute	Relative cumulative	
1	0	0	87811	0.878	-11.23 ± 0.72
2	Z	0	11481	0.993	-12.90 ± 0.92
3	0	1	614	0.999	-11.44 ± 0.84
4	0	Z	94	1.000	-17.74 ± 0.88

(b) Rate values and ancestral states at nodes PIH and PIE

Model category	Rate (mean ± SD)		Node PIH		Node PIE	
	q_{MP}	q_{PM}	p(M|node) ± SD	p(P|node) ± SD	p(M|node) ± SD	p(P|node) ± SD
1	3.10 ± 2.16	3.10 ± 2.16	0.79 ± 0.11	0.21 ± 0.11	0.93 ± 0.08	0.07 ± 0.08
2	0.00 ± 0.00	5.06 ± 2.00	0.00 ± 0.00	1.00 ± 0.00	0.00 ± 0.00	1.00 ± 0.00
3	2.60 ± 1.87	4.19 ± 3.26	0.72 ± 0.16	0.28 ± 0.16	0.84 ± 0.18	0.16 ± 0.18
4	3.71 ± 1.51	0.00 ± 0.00	1.00 ± 0.00	0.00 ± 0.00	1.00 ± 0.00	0.00 ± 0.00
All	2.74 ± 2.26	3.33 ± 2.24	0.70 ± 0.27	0.30 ± 0.27	0.83 ± 0.31	0.17 ± 0.31

* "Z" denotes rates assigned to the zero class. "0" and "1" denote two distinct non-zero rate classes; rates with the same value are assigned to the same non-zero rate class. For example, under model category 1 q_{MP} and q_{PM} are assigned to the same non-zero rate class, that is, they take the same positive value; under model category 2 q_{MP} is assigned to the zero rate class, that is, it is set to zero, while q_{PM} is assigned to a non-zero rate class, that is, it takes a positive value; under model category 3 q_{MP} and q_{PM} are assigned to distinct non-zero rate classes, that is, they take different positive values.

† The relative cumulative frequency of a model category is obtained by summing the absolute frequency of sampled points in the model category to the absolute frequencies of sampled points in all preceding categories, and then dividing by the total number of sampled points in all categories [e.g. $(87,811 + 11,481)/10^5 = 0.993$ for model category 2].

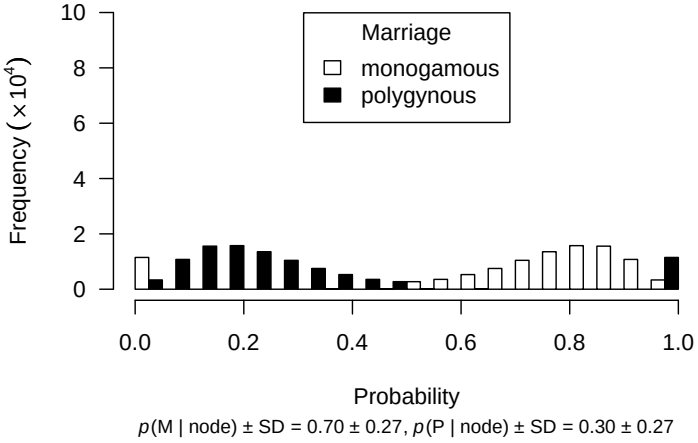


Figure 4.2: Posterior probability distributions of states M and P at node PIH.

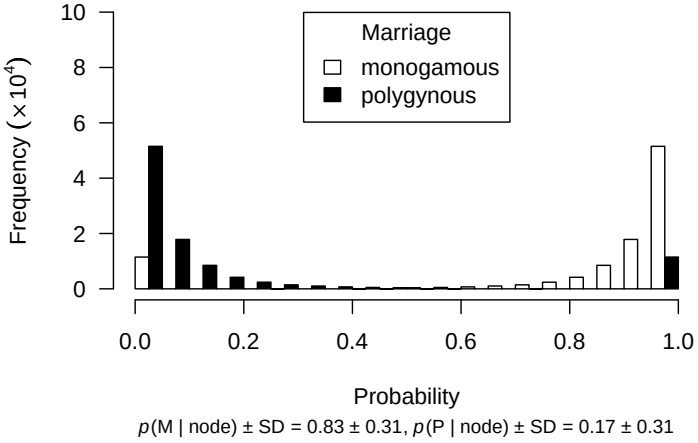


Figure 4.3: Posterior probability distributions of states M and P at node PIE.

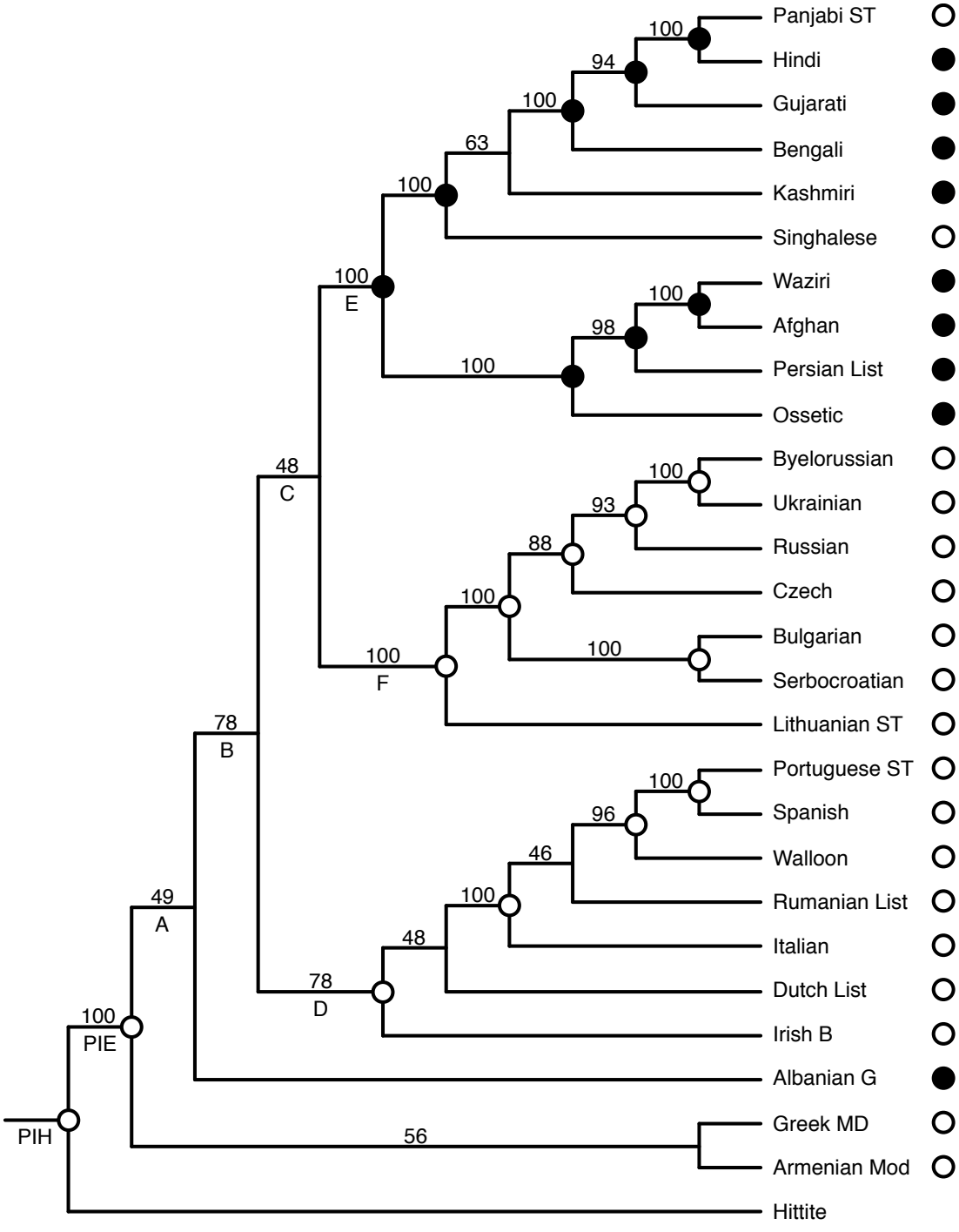


Figure 4.4: The consensus tree of Figure 4.1 for 27 IE speech varieties plus Hittite. The value above each node represents the node's posterior probability, p(node), as a percentage. Tips are colour-coded to represent the marriage strategy of the corresponding societies (white: monogamy; black: polygyny; Hittite was not assigned marriage strategy data). Nodes are colour-coded to represent the combined probabilities of the two states [white: $p(\mathrm{M}) \geq 0.70$; black $p(\mathrm{P}) \geq 0.70$; other nodes have combined probability < 0.70 for both states].

Table 4.2: Ancestral states of marriage strategy at selected nodes on the consensus tree

Node*†	p(node)	p(M|node) ± SD (range)	p(P|node) ± SD (range)
A	0.49	0.77 ± 0.29 (0.00–1.00)	0.23 ± 0.29 (0.00–1.00)
B	0.78	0.82 ± 0.31 (0.00–1.00)	0.18 ± 0.31 (0.00–1.00)
C	0.48	0.61 ± 0.21 (0.00–1.00)	0.39 ± 0.21 (0.00–1.00)
D	0.78	0.93 ± 0.08 (0.50–1.00)	0.07 ± 0.08 (0.00–0.50)
E	1.00	0.08 ± 0.09 (0.00–1.00)	0.92 ± 0.09 (0.00–1.00)
F	1.00	0.96 ± 0.04 (0.50–1.00)	0.04 ± 0.04 (0.00–0.50)

* The letters correspond to the node labels in Figure 4.4.
† The combined probabilities, p(M) and p(P), are obtained as $p(\text{M}) = p(\text{M}|\text{node}) \cdot p(\text{node})$ and $p(\text{P}) = p(\text{P}|\text{node}) \cdot p(\text{node})$ (Section 4.2.3).

The uncertainty in the reconstructions at the base of the consensus tree means that a host of scenarios can explain the distribution of states of marriage strategy at the tips (Figure 4.4). Polygyny was acquired at least once on the tree, between nodes PIE and E, and possibly a second time in the branch leading to Albanian G. A minimum of two reversals to monogamy occurred, one in the branch leading to Panjabi ST and one in the branch leading to Singhalese.

4.3.2 Fossilization of nodes PIH and PIE

At convergence, the chains fossilizing nodes PIH and PIE sampled states in the model of trait evolution as shown in Table 4.3 (Section C.3).

Comparison of the $\log_e[H(\text{likelihood})]$ values yields $2\log_e(B_{\text{MP}}) \approx 1.66$ at node PIH (Table 4.3a), corresponding to no evidence for monogamy over polygyny by the conservative criteria used, and $2\log_e(B_{\text{MP}}) \approx 3.35$ at node PIE (Table 4.3b), corresponding to positive evidence for monogamy over polygyny.

Overall, these results confirm the ancestral state estimates obtained with nodes not fossilized (Section 4.3.1.2); in particular, the magnitude of the evidence for monogamy at node PIE reflects the strong skew towards high values for state M in the posterior probability distribution (Figure 4.3).

Table 4.3: Summary parameters for the samples returned by the fossilization chains

(a) Node PIH

Parameter	Fossil state	
	M	P
Mean $\log_e$(likelihood) ± SD	-11.44 ± 0.78	-12.82 ± 0.80
Range of $\log_e$(likelihood) values	-20.91 to -9.91	-21.05 to -10.74
Autocorrelation coefficient r	0.001	-0.001
Mean acceptance rate	21.0%	24.8%
$\log_e[H(\text{likelihood})]$	-12.60	-13.43

(b) Node PIE

Parameter	Fossil state	
	M	P
Mean $\log_e$(likelihood) ± SD	-11.27 ± 0.76	-13.19 ± 1.01
Range of $\log_e$(likelihood) values	-21.07 to -9.94	-21.98 to -10.74
Autocorrelation coefficient r	-0.001	0.001
Mean acceptance rate	21.3%	25.1%
$\log_e[H(\text{likelihood})]$	-12.38	-14.05

4.4 Discussion

The phylogenetic comparative analysis of marriage strategies across societies speaking IE languages provides evidence in support of PIE monogamy; this pattern likely extended back to PIH, but the evidence is only suggestive. Polygyny evolved at least once, possibly twice, throughout the history of IE-speaking societies, but uncertainty in some of the "deep" reconstructions means that alternative evolutionary scenarios cannot be excluded. This uncertainty emphasizes the need for an explicitly historical approach when deriving inferences about past social organization from cross-cultural data, and to cross-cultural comparison more generally. In turn, the uncertainty in the phylogenetic model used to represent how the societies are related by descent stresses the importance of avoiding "best tree" approaches in phylogenetic comparative analysis.

As discussed in Section 4.1.2, Fortunato and Mace (2009) used a "best" tree in the phylogenetic comparative analysis of marriage strategies and strategies of wealth transfer at marriage in IE-speaking societies. The present findings suggest that their reconstruction of PIH monogamy is not contingent upon the phylogenetic tree used. Further, while the outgroup Hittite was not assigned marriage strategy data in the present analysis (Section 4.2.2), it was coded as monogamous in Fortunato and Mace's (2009); this was necessary because the phylogenetic comparative method they used did not allow missing data (Pagel n.d.).[1] The present findings indicate that the reconstruction by Fortunato and Mace (2009) is not contingent upon the state they assigned to the outgroup. Applying a phylogenetic comparative approach to the

[1]The marriage strategy coding for Hittite in Fortunato and Mace (2009) was based on information from the Hittite code of laws, a compendium of approximately 200 clauses dating back to at least 1650 BCE (Bryce 2002, p. 34). Several clauses of the code deal with marriage and with the property and inheritance rights of spouses and their offspring; the fact that no reference is made to multiple wives in this context suggests that only monogamous marriages were officially recognized (Bryce 2002, pp. 132–133). However, the code also stipulates that a man's widow be married to his brother, father, or father's brother (Bryce 2002, p. 131; Gurney 1975, p. 101; Hoffner 1997, p. 152). The relevant clause does not specify that the widow be married to a wifeless kinsman, thus it is possible — and indeed likely in the case of marriage to the man's father or father's brother — that this provision resulted in polygynous unions (Bryce 2002, p. 132). Finally, the Hittite king was expected to supply the kingdom with royal progeny to fulfil political, administrative, and diplomatic office, a reproductive onus accomplished through a harem of secondary wives and concubines (Bryce 2002, pp. 27–29). This suggests that polygynous mating, if not polygynous marriage, was sanctioned in at least one case; however, there is no evidence to indicate that this applied to other members of Hittite society (Bryce 2002, p. 132).

marriage transfer strategy data, in a Bayesian MCMC framework, Fortunato et al. (2006) showed that the reconstruction of PIH dowry is similarly robust to phylogenetic tree model and coding of the outgroup.

More generally, these reconstructions push the origin of monogamous marriage into prehistory, well beyond the earliest instances documented in the historical record. This implies that the archaeological and genetic evidence for the nuclear family in prehistoric populations may reflect a monogamous marriage strategy; on their own, the archaeological and genetic data can at best provide clues about a monogamous *mating* pattern. For example, Haak et al. (2008) found evidence, through analysis of aDNA samples, of genetic relatedness of one adult male and one adult female with two children recovered in one burial at the site of Eulau, Germany, a late Neolithic community (*c.* 2600 BCE) attributed to the Corded Ware culture; they argued that this establishes "the presence of the classic nuclear family in a prehistoric context in Central Europe" (Haak et al. 2008, p. 18229). Similarly, Bentley et al. (2008) identified a nuclear family, comprising an adult male, an adult female, a mature female, and two children, through analysis of the isotopic signatures of skeletal remains in the communal grave at Talheim, Germany, an early Neolithic community (*c.* 4900–4800 BCE) attributed to the Linear Ware culture; previous analysis of the teeth had revealed high similarity between the male and the children, suggestive of genetic relatedness. The Corded Ware and Linear Ware cultures are archaeological horizons of northern and central Europe associated with populations speaking IE languages (Mallory 1997a,b). The phylogenetic comparative analysis in this chapter shows that monogamous marriage prevailed among prehistorical IE-speaking societies located in Europe. At least to the extent that evidence from a single grave can substantiate claims such as Haak et al.'s (2008), this suggests that the burial patterns may reflect the monogamous marriage strategy of the Eulau and Talheim communities.

Larger-scale analyses of Y-chromosome data provided evidence for a later increase in effective male population size compared to effective female population size, across European (Dupanloup et al. 2003; Pereira et al. 2001) and worldwide (Dupanloup et al. 2003) samples. One possible interpretation of this pattern is that the difference in effective populations was caused by a regime of polygynous mating, which resulted in greater variance in reproductive success for males than for females (Dupanloup et al. 2003; Pereira et al. 2001). Further, Dupanloup et al. (2003) interpreted the delayed

increase in the effective male population as evidence for a relatively recent shift from polygynous to monogamous mating; based on Pritchard et al.'s (1999) estimates for the timing of expansion of Y-chromosome data, they linked this shift to the emergence of food production, between 10,000 and 5000 years ago in Europe and Asia and more recently elsewhere, when "Nuclear families replaced the polygamous, extended-family compounds typical of hunting-gathering populations" (Dupanloup et al. 2003, p. 96).[1] The reconstruction of PIE monogamy presented in this chapter, with monogamy likely extending back to PIH, falls within this temporal interval (Section 4.1.1), suggesting that monogamous marriage had emerged in Eurasia by that time. However, Dupanloup et al.'s (2003) interpretation holds only to the extent that the shift to the "nuclear family", i.e. from polygynous to monogamous marriage, coincided with a shift from polygynous to monogamous mating, with consequent reduction in the variance in male reproductive success. As noted in Section 2.1, the historical and ethnographic evidence suggest that variance in male reproductive success is comparable in societies practising monogamous and polygynous marriage.

Finally, and most importantly, the phylogenetic comparative analysis confutes explanations linking the emergence of monogamous marriage to the development of features of social organization typically associated with "complex", "modern" societies located in Eurasia. The work presented in Chapters 2 and 3 situates variation in marriage strategies in the context of variation in ecological factors, linking the prevalence of monogamy across Eurasian societies to the development of intensive modes of production. Diamond (1998) has convincingly argued that the relative greater "complexity" of these societies, and their consequent "modernization", can also be attributed to ecological determinants that facilitated the emergence of food production in the region. This raises the possibility that ecological factors act as a confounding variable in the observed relationship between marriage strategies and indicators of "societal complexity" and "modernization". An appeal to "complexity" and "modernization" as the terminus of explanation amounts to providing a proximate answer to ultimate questions about the evolution of marriage strategies.

[1] As discussed in Section 1.2.3.2, technically the "nuclear family" exists in societies practising monogamous and polygamous marriage. Instead, Dupanloup et al. (2003) use the concept as synonymous with non-extended and monogamous family organization.

Chapter 5

Reconstructing the history of residence strategies in Indo-European-speaking societies

5.1 Introduction

5.1.1 Background

Residence strategies regulate the dispersal of individuals at marriage; like dispersal strategies in other species, they determine the pattern of differential access of individuals to kin (Strier 2008). By structuring the spatial arrangement of individuals within groups, this feature of social organization represents one key factor influencing the pattern of co-operation and competition among relatives within groups (Section 6.1). Reconstructing the history of residence strategies is thus crucial to understanding the evolution of human social behaviour. In anthropology, the notion of the centrality of residence to social structure is captured by the influential theory, advanced by Lowie (1920) and formalized by Murdock (1949, pp. 221–222), according to which changes in residence drive changes in descent system and kinship terminology (see review in Levinson and Malone 1980, pp. 105–113).

In this chapter I reconstruct the pattern of change in residence strategies in the history of societies speaking IE languages, using the phylogenetic comparative approach outlined in Chapter 4; in Chapter 6 I use this approach to investigate the co-evolutionary interactions of residence strategies with marriage strategies in

IE-speaking societies. Accurate inference of early IE residence is also important for correctly describing the homeland and trajectory of dispersal of the IE language family: reconstructions of this aspect of social organization have been used in linguistics and archaeology to constrain hypotheses about the origin and spread of IE languages (Section 1.2.3.2). For example, Gimbutas (1991) excluded Anatolia and south-eastern and central Europe as potential IE homelands because the Neolithic communities living in these regions were "matrifocal", whereas early IE society was reconstructed as patrilineal and patrilocal (cited in Mallory 1997c, p. 483).

Definitions of residence strategies have varied across time and across authors, and this has generated considerable confusion in the literature (Levinson and Malone 1980, pp. 100–101; e.g. Goodenough 1956; Murdock 1962). For example, in the *EA* Murdock (1967b) terms residence with or near the husband's male patrilineal kin "patrilocal" if the patrikin are aggregated in patrilocal and patrilineal groups, "virilocal" if they are not. In contrast, Fox (1967, p. 84) uses "patrilocal" for residence with the husband's father, and "virilocal" for residence with the husband's group more generally. The degree of terminological sophistication implicit in these definitions seems redundant in the absence of theoretical justification: all scenarios involve the movement of wives to their husband's kin at marriage, as opposed to the movement of husbands to their wife's. Therefore, I follow Keesing (1975, p. 37) in using "virilocality" for residence with or near the husband's kin, "uxorilocality" for residence with or near the wife's kin, and "neolocality" for residence apart from the kin of either spouse; this usage is preferable because it reflects the literal meaning of the terms (Parkin 1997, p. 31). However, use of the simpler definitions does not imply that residence is unrelated to other aspects of social organization; rather, by focusing on the spatial arrangement of individuals within groups, it avoids incorporating in the analyses any unnecessary assumptions about these relationships that may be built into the convoluted categorizations.

5.1.2 Related research

Like marriage strategies (Section 4.1.2), early IE residence strategies have been reconstructed on the basis of linguistic and ethnographic evidence. The linguistic evidence is more substantial in this case, but its interpretation has been strongly biased towards virilocality by the purportedly "male-centred" structure of early IE society (Clackson 2007, pp. 201–206; e.g. Anthony 2007, p. 92). I discuss the linguistic arguments in

detail to highlight the "anthropological absurdity" (Szemerényi 1977, p. 196) of some of the conclusions drawn from them.

Much of the discussion about early IE residence revolves around the reconstructed terminology for affines (in-laws) (reviewed in Clackson 2007, pp. 201–206). Terms that can be related to the PIH form are used in Indo-Iranian, Latin, Germanic, Celtic, and Albanian languages for the in-laws of husband and wife, but only for wife's in-laws in Greek, Slavic, Baltic, and Armenian languages. One possible interpretation of this pattern is that the original terms were used in PIH for the in-laws of husband and wife, and that Greek, Slavic, Baltic, and Armenian languages independently developed terms for husband's in-laws (Hettrich 1985; Szemerényi 1977). The use of one set of terms for both classes of affines in PIH is explained by assuming that PIH residence was neolocal, such that husbands and wives had equal access to their in-laws. In turn, the fact that the terms related to the PIH form are invariably used for wife's in-laws in Greek, Slavic, Baltic, and Armenian languages is explained by assuming that the shift in meaning was caused by a shared change in social structure. For example, a transition from neo- to virilocality in the ancestor of speakers of these languages would explain the restriction in meaning of the PIH-derived terms to wife's in-laws: if the wife joined her husband's kin at marriage, she would have greater contact with her in-laws than the husband with his; this would result in wives eventually co-opting the original PIH terms for designating their in-laws (Clackson 2007, p. 205). Consistent with this scenario, languages using derivatives of the reconstructed PIH terms for wife's in-laws only are located at the centre of the IE geographic range; with the exception of Albanian, languages using derivatives of the reconstructed terms for affines on both sides are located on its eastern and western edges (Clackson 2007, p. 205; Hettrich 1985).

An alternative interpretation prevails in the literature, following Delbrück (1889), which posits that PIH speakers used the original terms only for wife's in-laws. The fact that no specific terms can be reconstructed for husband's in-laws is explained by assuming that affines in this class were designated in PIH through generic terms: for example, Greek uses a generic term for wife's father, wife's brother, and daughter's husband. In turn, the use of generic terms for husband's in-laws is explained by assuming that PIH residence was virilocal: if the wife joined her husband's kin at marriage, the husband would have limited contact with his wife's kin and would not

need specific terms to designate them (Clackson 2007, pp. 201, 205). Consistent with this scenario, the reconstructed PIH term for the verb "lead" is related to the Indo-Iranian term for "bride" (attested in Avestan, Iranian sub-group, first millennium BCE, and in Sanskrit, Indic sub-group, *c.* 1000 CE onwards) and to terms used in languages belonging to the North-Western group to indicate the act of becoming married from the male perspective (attested in New English, Germanic sub-group, *c.* 1500 CE onwards; in New Welsh, Celtic sub-group, *c.* 1500 CE onwards; in Old Prussian, Baltic sub-group, *c.* sixteenth to eighteenth centuries CE; and in Lithuanian, Baltic sub-group, *c.* eighteenth century CE onwards) (Mallory and Adams 2006, p. 207). This suggests that the PIH bride was "led away" at marriage to join the house of her husband or husband's kin (e.g. Mallory 1989, pp. 83, 123). However, the use of terms for "lead" in the context of marriage may relate to some aspect of the wedding ceremony rather than to residence customs (Clackson 2007, p. 205). Further, residence of the wife in the house of her husband constitutes virilocality if the husband resides with his (father's) kin, and neolocality otherwise (Section 5.1.1). This terminological confusion likely stems from an obsolete definition of residence strategies that subsumes both cases, the former as "viripatrilocality", under "patrilocality" (e.g. Szemerényi 1977).

More importantly, all of the 137 terminologies listed in Morgan's (1871) *Systems of consanguinity and affinity of the human family* include specific terms for at least some of the husband's in-laws (Goody 1959). Thus, a system like the one ascribed to PIH under this scenario, lacking specific terms for all of the husband's affines, is not attested in the ethnographic record. The terminology that more closely resembles the system reconstructed for PIH obtains among the Laguna of the Western Pueblos, who have a specific term for "husband's father" but not for "wife's father", and no recorded terms for "wife's siblings". Ironically, however, the Laguna lack a specific term for "wife's father" because they are uxorilocal (and matrilineal): husbands marry in and designate their father-in-law as "father". On this evidence, the only plausible conclusion that can be drawn from the prevailing reconstruction of PIH affinal terminologies is that PIH society was uxorilocal (and matrilineal). It comes as no surprise, then, that supporters of the "male-centred" structure of early IE society should omit Goody's (1959) careful analysis from their discussions of early IE residence (e.g. Mallory 1997c).

If bias in interpretation of the linguistic evidence can be attributed to the excessive reliance of Indo-Europeanists on "the discarded hypotheses of social anthropology"

(Goody 1959, p. 91), bias in interpretation of the ethnographic data can be attributed to their reliance on discarded methods. For example, Mallory (1997c, p. 483) adduces the prevalence of virilocality among the historically attested IE-speaking societies in favour of this residence strategy for early IE society. However, distributional reasoning of this type, based on unsystematic and ahistorical use of the ethnographic evidence, can easily lead to spurious inference about the history of cultural practices (Fortunato 2008; Fortunato et al. 2006; Section 4.1).

Murdock's (1949, p. 349) reconstruction, based on the distribution of aspects of social organization across societies speaking languages belonging to the major divisions of the IE family, was discussed in Section 4.1.2. The Eskimo system of social organization attributed to early IE society under this reconstruction features neolocality in its typical form and non-neolocal residence in its variant sub-types.

5.1.3 Rationale and objective

As with marriage strategies (Section 4.1.3), previous reconstructions of early IE residence strategies have relied on unsystematic and ahistorical use of the linguistic and ethnographic evidence. Additionally, in this case inferences have been plagued by substantial bias in interpretation.

The phylogenetic comparative approach used in Chapter 4 provides a systematic and explicitly historical framework for investigating cross-cultural variation (Section 1.2.3.2). Here I use this approach to reconstruct the pattern of change in residence strategies in the history of IE-speaking societies, and to formally evaluate one of the scenarios derived from the linguistic evidence (Section 5.1.2). Assuming that PIH speakers used the same terms for the in-laws of husbands and wives, the shared restriction in meaning in Greek, Slavic, Baltic, and Armenian languages, in which PIH-derived terms are used only for wife's in-laws, has been attributed to a shared transition from neo- to virilocality. I reconstruct the residence strategy for the ancestor of speakers of these languages and, for comparison, for the ancestor of speakers of Indo-Iranian, Latin, Germanic, Celtic, and Albanian languages, in which PIH-derived terms are used for the in-laws of both husbands and wives. If the former did indeed experience a shift from neo- to virilocality, the reconstructions at the two nodes should differ substantially.

5.2 Data and methods

Following the procedure set out in Section 4.2, I used data on residence strategy from the *EA* (Gray 1999; Murdock 1967b) for a sample of 27 IE-speaking societies (Section 5.2.1), mapped onto Pagel et al.'s (2007) sample of trees (Section 5.2.2). On the cross-cultural data and tree sample, I used the phylogenetic comparative method implemented in BayesMultistate to reconstruct ancestral states of residence strategy (Section 5.2.3).

5.2.1 Cross-cultural data

I obtained the cross-cultural sample as described in Section 4.2.1. The data in binary form and maps of their geographical distribution are in Section B.2.

The *EA* scores societies separately for prevailing and alternative modes of residence (variables 12 and 14, respectively; Gray 1999), the latter defined as "culturally patterned alternatives to, or significant deviations from, the prevailing profile" (Murdock 1967b, p. 156); a strategy is defined as prevailing when it exceeds the other in frequency by a ratio greater than 2 to 1. I included information from both variables in the analyses, thus addressing the persistent criticism of cross-cultural research that this approach ignores intra-societal variability in cultural practices (Burton and White 1987; Levinson and Malone 1980, p. 9). In order to give higher weight to the prevailing mode of residence, I assigned each society three columns of data: two identical columns specifying the prevailing pattern and a third column specifying the alternative pattern (Section 5.2.3). The prevailing mode was used at all three columns for societies scored as not presenting an alternative mode. This arbitrary weighting scheme broadly captures the definitions of prevailing and alternative modes of residence used in the *EA* codes.

For each mode of residence, I coded societies as neolocal (state N), uxorilocal (state U), or virilocal (state V), as defined in Section 5.1.1. State V subsumed both cases in which the husband's male patrilineal kin are aggregated in patrilocal and patrilineal groups, and cases in which they are not; as noted in Section 5.1.1, these are termed respectively "patrilocal" and "virilocal" in the *EA*. I used the dual state UV for ambilocal societies, in which residence is established optionally with (or near) the kin of either spouse and with approximately equal frequency (Murdock 1967b; Section 5.2.3). For example, the Afghans are scored in the *EA* as practising patrilocality with no alternative, and were coded "V, V, V". The Byelorussians are scored as

practising prevailing ambilocality with alternative neolocality, and were coded "UV, UV, N". The Greeks are scored as practising prevailing virilocality with alternative neolocality, and were coded "V, V, N". This produced a sample with 2 (7.4%) of 27 societies coded as practising prevailing ambilocality (both practising alternative neolocality), 5 (18.5%) coded as practising prevailing neolocality (with 1 practising alternative uxorilocality and 1 practising alternative virilocality), and 20 (74.1%) coded as practising prevailing virilocality (with 9 practising alternative neolocality and 2 practising alternative uxorilocality) (Table B.2 and Figures B.2c and B.2d).

5.2.2 Tree sample

I obtained the tree sample as described in Section 4.2.2. The outgroup Hittite was assigned no residence strategy data for the purpose of the comparative analysis (Section 5.2.3).

5.2.3 Comparative analysis

As discussed in Section 4.2.3, BayesMultistate uses the cross-cultural data and tree sample to estimate parameters in the model of trait evolution (Section C.1). In this case the comparative data consisted of three "sites", two representing the prevailing mode of residence and one representing the alternative mode, each taking three states (N, U, V) (Section 5.2.1). In analyses with multiple sites, BayesMultistate uses information from the sites simultaneously to estimate a single set of rate parameters specifying the model of trait evolution. Three states require six rate parameters — in this case, q_{NU}, q_{NV}, q_{UN}, q_{UV}, q_{VN}, q_{VU}.

As noted in Section 4.2.3, in the likelihood calculations BayesMultistate treats taxa that are not assigned comparative data, like the outgroup Hittite in this case (Section 5.2.2), as taking any state with equal probability. Similarly, BayesMultistate treats taxa that are assigned multiple states at a site as taking those states with equal probability at the relevant site; this applied to the two societies that were assigned the dual state UV, representing ambilocality. BayesMultistate's treatment of these cases is consistent with the definition of ambilocality, where residence with husband's or wife's kin occurs with approximately equal frequency (Section 5.2.1).

As discussed in Section 4.2.3, in Bayesian RJ-MCMC mode BayesMultistate uses RJ-MCMC chains to produce a posterior probability sample of states in the model of trait

evolution (Sections C.1 and C.2). I performed eight sets of analyses, each comprising five separate chains started from random seeds (Section C.3). One set estimated the posterior probability distributions of states N, U, and V at internal nodes on the consensus tree summarizing the tree sample; the chains returned separate distributions for prevailing and alternative modes of residence. The means of the posterior probability distributions of states N, U, and V for a given node, p(N|node), p(U|node), and p(V|node), are multiplied by the posterior probability of the node, p(node), to produce the combined probabilities of the three states at the node, p(N), p(U), and p(V); p(N|node) + p(U|node) + p(V|node) = 1, thus p(N) + p(U) + p(V) = p(node). As noted in Section 4.2.3, the value of p(node) sets an upper limit on the confidence that can be placed in the reconstructions at the node. As a rule of thumb, confidence can be placed in reconstructions with combined probabilities ≥ 0.70.

A further six sets of analyses fossilized nodes PIH and PIE: for each node, one set of analyses was run with the node fixed to state N, one with the node fixed to state U, and one with the node fixed to state V. BayesMultistate does not allow sites to be fossilized separately, therefore each run fixed all three sites to the same state. As discussed in Section 4.2.3, the fossilization procedure is used to assess the relative "fit" of the alternative states at a node; in this case, the chains returned a single posterior probability distribution of $\log_e$(likelihood) values, which effectively "averaged" the fit of the fossil state at the node across the three sites. I used the Bayes factor procedure described in Section 4.2.3 to assess the strength of the evidence in favour of one state over another at a given node.

The final set of analyses used BayesMultistate's "most recent common ancestor" (MRCA) approach to estimate the posterior probability distributions of states N, U, and V at two nodes. One node represented the ancestor of societies speaking languages in which PIH-derived terms are used only for wife's in-laws (Greek, Slavic, Baltic, and Armenian languages); the other represented the ancestor of societies speaking languages in which PIH-derived terms are used for in-laws on both sides (Indo-Iranian, Latin, Germanic, Celtic, and Albanian languages). I denote these nodes "CORE" and "EDGE", respectively, to reflect the geographic distribution of the two sets of languages (Section 5.1.2 and Table 5.1). As discussed in Section 5.1.3, one scenario derived from the linguistic evidence assumes that a transition from neo- to virilocality occurred in the ancestor of the first set of societies (corresponding to node CORE); a difference in

Table 5.1: Speech varieties included in the MRCAs

MRCA	Sub-group*	Speech variety†
CORE	Armenian	Armenian Mod
	Baltic	Lithuanian ST
	Greek	Greek MD
	Slavic	Bulgarian, Byelorussian, Czech, Russian, Serbocroatian, Ukrainian
EDGE	Albanian	Albanian G
	Celtic	Irish B
	Germanic	Dutch List
	Indo-Iranian	Afghan, Bengali, Gujarati, Hindi, Kashmiri, Ossetic, Panjabi ST, Persian List, Singhalese, Waziri
	Latin	Italian, Portuguese ST, Rumanian List, Spanish, Walloon

* After Clackson (2007, p. 201).

† After Dyen et al. (1992).

the reconstructions at the two nodes, reflecting the shift in residence strategies at node CORE, would provide evidence for this scenario. By definition, a node representing the MRCA of a set of taxa exists in all trees in a tree sample: in some it includes only the taxa of interest, while in others it includes additional taxa besides the taxa of interest. Therefore, MRCAs have $p(\text{node}) = 1$, such that $p(\text{N}|\text{node}) = p(\text{N})$, $p(\text{U}|\text{node}) = p(\text{U})$, and $p(\text{V}|\text{node}) = p(\text{V})$ at nodes CORE and EDGE. The chains returned separate posterior probability distributions for prevailing and alternative modes of residence.

I determined the RJ-MCMC chain specifications through preliminary maximum-likelihood and MCMC runs, all with nodes not fossilized. As noted in Section 4.2.3, these specifications ensure that the RJ-MCMC chains sample parameter space adequately and ultimately converge to the posterior probability distribution of states in the model of trait evolution (Section C.3). I ran the RJ-MCMC chains for 10^8 iterations, sampling every 10^3, with an additional burn-in of 10^6, and rate deviation set to 30. Under maximum-likelihood the covarion model for trait evolution improved the mean $\log_e$(likelihood) by 2.6 units, and was therefore implemented by the RJ-MCMC chains; this model allows rates to vary within and between branches of a tree. All chains used a uniform prior on the models and an exponential prior on the rate parameters; the

mean of the exponential prior was seeded from a uniform hyperprior on the interval 0–10. The shape of the prior distribution (exponential or gamma) and the interval of the hyperprior (0–10 or 0–20) only marginally affected the mean of the posterior probability distributions of $\log_e$(likelihood) values and of ancestral states, returning qualitatively similar results.

Convergence of the chains to the target distributions and near-independence of sampling events were assessed as described in Section 4.2.3. In all cases, the diagnostics indicated that the chains sampled the target distributions adequately.

5.3 Results

For each set of analyses, I compared the $\log_e[H(\text{likelihood})]$ values for the states in the model of trait evolution sampled by the separate chains at convergence; I present results for the chain that returned the median value of the $\log_e[H(\text{likelihood})]$.

I discuss the ancestral state estimation at nodes on the consensus tree in Section 5.3.1, the fossilization of nodes PIH and PIE in Section 5.3.2, and the ancestral state estimation at the MRCAs in Section 5.3.3.

5.3.1 Estimation of ancestral states on the consensus tree

At convergence, the chain sampled states in the model of trait evolution with mean $\log_e$(likelihood) $\pm$ SD $= -44.13 \pm 1.61$ (range: -55.47 to -39.87; auto-correlation coefficient: $r = 0.017$; mean acceptance rate: 28.8%; Section C.3).

I discuss separately the posterior probability distribution of model categories returned by the chain (Section 5.3.1.1) and the ancestral state estimates over all model categories (Section 5.3.1.2).

5.3.1.1 Posterior probability distribution of model categories

The chain sampled 268 model categories, with rates assigned to 1.76 ± 0.46 non-zero classes (mean $\pm$ SD; range: 1–4 non-zero classes). Therefore, some of the evolutionary transitions specified by the six rate parameters are not required for explaining the observed distribution of states of residence strategy across societies in the sample. This is illustrated by Table 5.2, which presents the ten model categories sampled most frequently by the chain, accounting for 73.2% of the 10^5 sampled points; the

Table 5.2: Rate classes and frequencies for selected model categories

Model category	Rate class*						Frequency†	
	q_{NU}	q_{NV}	q_{UN}	q_{UV}	q_{VN}	q_{VU}	Absolute	Relative cumulative
1	0	0	0	0	0	Z	17209	0.172
2	0	0	0	0	1	Z	15793	0.330
3	0	1	1	1	0	Z	10163	0.432
4	0	1	1	Z	0	Z	6253	0.494
5	0	0	0	Z	0	Z	5638	0.551
6	0	1	1	0	0	Z	4997	0.601
7	0	0	0	Z	1	Z	3617	0.637
8	0	0	0	1	1	Z	3349	0.670
9	0	0	1	0	1	Z	3084	0.701
10	0	0	Z	0	1	Z	3083	0.732
⋮								⋮
100	Z	0	0	0	0	0	14	0.994

* "Z" denotes rates assigned to the zero class. "0" and "1" denote two distinct non-zero rate classes; rates with the same value are assigned to the same non-zero rate class. For example, under model category 1 q_{NU}, q_{NV}, q_{UN}, q_{UV}, and q_{VN} are assigned to the same non-zero rate class, that is, they take the same positive value, while q_{VU} is assigned to the zero rate class, that is, it is set to zero.

† The relative cumulative frequency of a model category is obtained by summing the absolute frequency of sampled points in the model category to the absolute frequencies of sampled points in all preceding categories, and then dividing by the total number of sampled points in all categories [e.g. $(17,209 + 15,793)/10^5 = 0.330$ for model category 2].

hundredth most frequently sampled category is included for comparison. In the top ten model categories rate parameter q_{VU} was always set to zero, while the other five rate parameters were set to zero or assigned to one or two non-zero classes.

Consistently, over all model categories the mean value of q_{VU} was an order of magnitude smaller than the mean values of the other five rate parameters (Figure 5.1). q_{VU} specifies transitions from viri- to uxorilocality; uxorilocality is observed only in the two ambilocal societies, Byelorussian and Dutch List, as prevailing mode of residence, and as alternative mode in Singhalese, Italian, and Armenian Mod (Table B.2 and Section 5.3.1.2). This suggests that the acquisition of uxorilocality is more likely

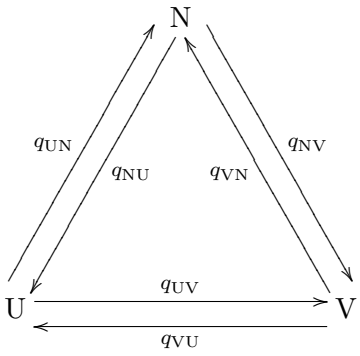


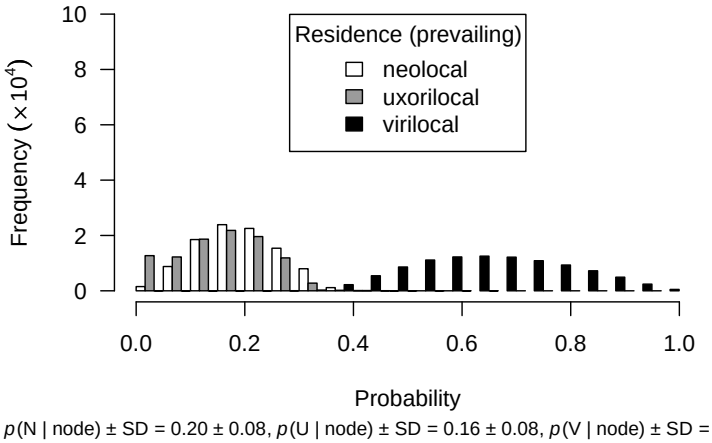
Figure 5.1: Rate parameters describing the evolution of residence strategy. Over all model categories, the mean ± SD is 5.93 ± 3.80 for q_{NU}, 8.50 ± 4.92 for q_{NV}, 7.98 ± 5.87 for q_{UN}, 6.35 ± 5.44 for q_{UV}, 3.89 ± 1.81 for q_{VN}, and 0.16 ± 0.68 for q_{VU}.

to have occurred through neolocality than through virilocality throughout the history of societies in the sample.

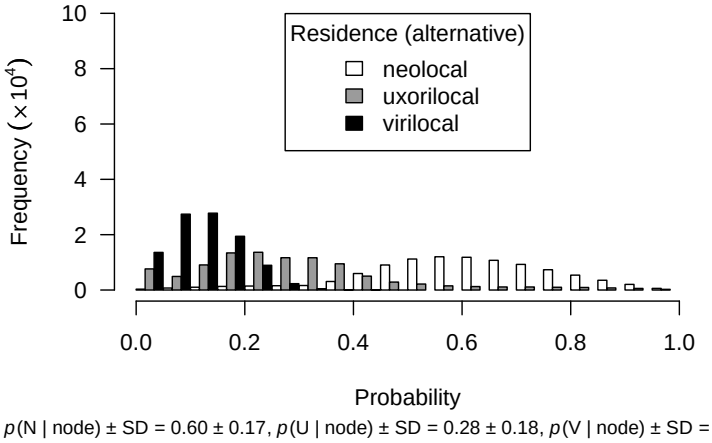
5.3.1.2 Posterior probability distributions of ancestral states

Over all model categories, node PIE reconstructed as prevailing virilocality and alternative neolocality with high posterior probabilities; reconstructions for node PIH were in the same direction but less certain (Figures 5.2 and 5.3). The posterior probability distributions are more strongly skewed towards high values for state V (as prevailing mode) and state N (as alternative mode) at node PIE, as reflected in the higher values of, respectively, $p(\mathrm{V}|\mathrm{node})$ and $p(\mathrm{N}|\mathrm{node})$ at this node.

Prevailing virilocality and alternative neolocality reconstructed with high posterior probabilities through to nodes A, B, and C on the consensus tree summarizing the tree sample, but phylogenetic uncertainty limits the confidence that can be placed in these inferences (Figure 5.4 and Table 5.3). Node D (the common ancestor of societies speaking Italic, Germanic, and Celtic languages) reconstructed as alternative neolocality with high posterior probability, but this inference is similarly affected by phylogenetic uncertainty. Node E (the common ancestor of societies speaking Indian and Iranian languages) reconstructed as prevailing virilocality with high posterior probability. Node F (the common ancestor of societies speaking Baltic and Slavic

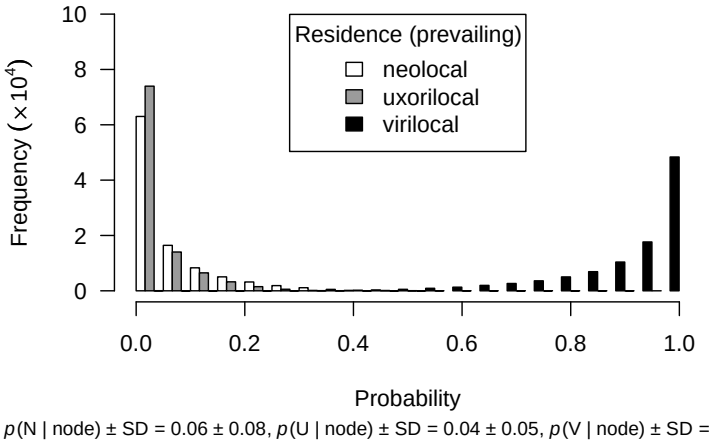


(a) Prevailing mode

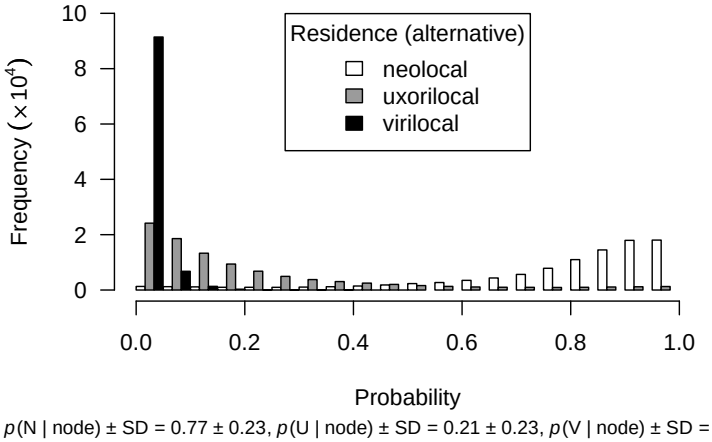


(b) Alternative mode

Figure 5.2: Posterior probability distributions of states N, U, and V at node PIH.



(a) Prevailing mode



(b) Alternative mode

Figure 5.3: Posterior probability distributions of states N, U, and V at node PIE.

languages) reconstructed as prevailing virilocality and alternative neolocality with high posterior probabilities.

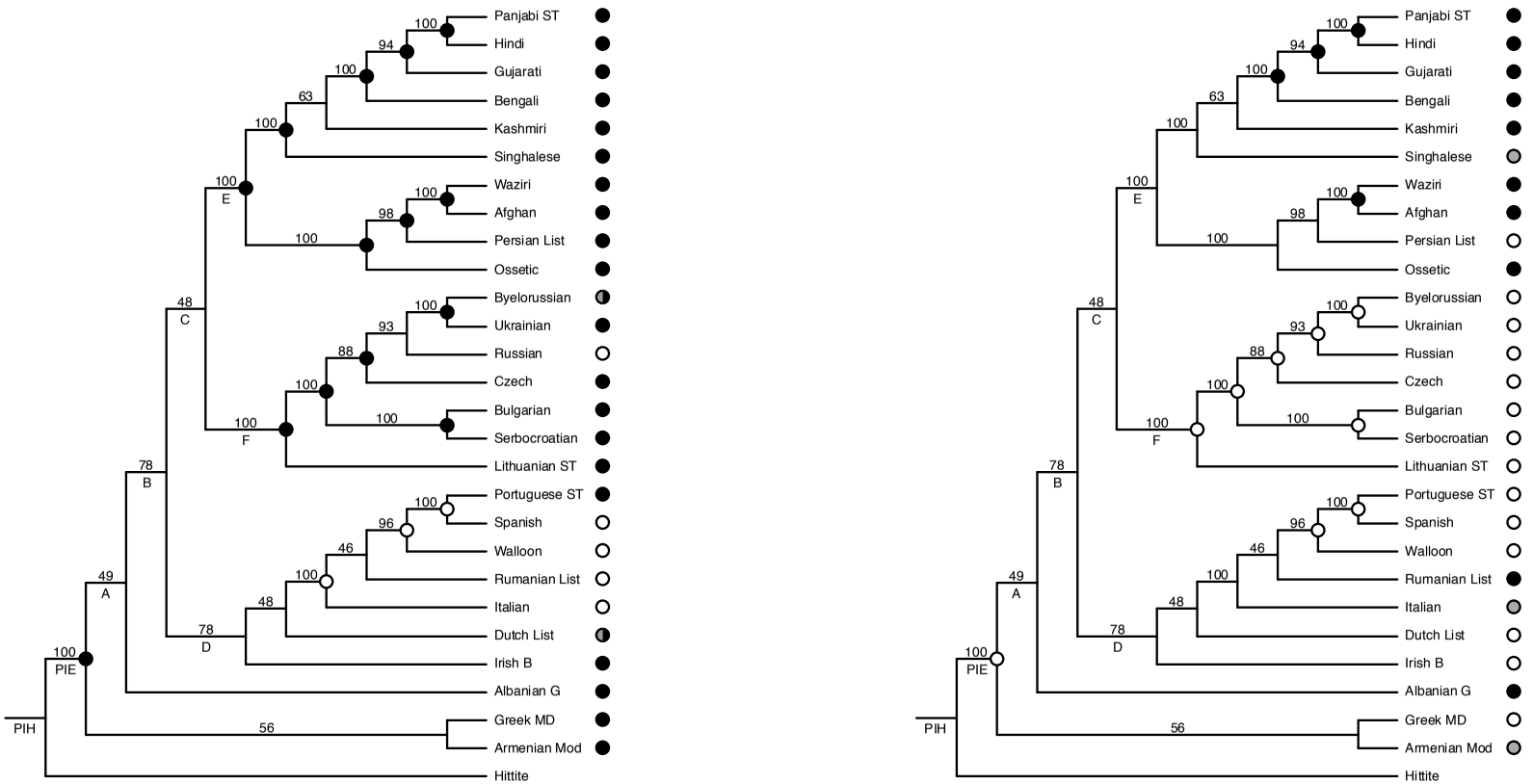
The uncertainty in the reconstructions at basal nodes on the consensus tree, coupled with uncertainty at more distal nodes, makes this pattern compatible with a wide range of evolutionary scenarios, for both modes of residence. As prevailing mode (Figure 5.4a), neolocality was acquired at least twice on the tree, once in the branch leading to Russian and once in the ancestor of societies speaking Italic languages (Portuguese ST, Spanish, Walloon, Rumanian List, Italian), and possibly a third time in the branch leading to Rumanian List. Uxorilocality was acquired twice, once in the branch leading to Byelorussian and once in the branch leading to Dutch List, resulting in ambilocality in both cases; this may have involved a transition from viri- to uxorilocality in the branch leading to Byelorussian (Section 5.3.1.1). At least one transition occurred from neo- to virilocality, in the branch leading to Portuguese ST. Formulation of an evolutionary scenario for alternative mode is made difficult by the additional uncertainty in the reconstructions at several internal nodes on the consensus tree (Figure 5.4b); in any case, uxorilocality was acquired at least three times, once in the branch leading to Singhalese, once in the branch leading to Italian, and once in the branch leading to Armenian Mod. As discussed in Section 5.3.1.1, the acquisition of uxorilocality is more likely to have occurred through neolocality than through virilocality.

5.3.2 Fossilization of nodes PIH and PIE

At convergence, the chains fossilizing nodes PIH and PIE sampled states in the model of trait evolution as shown in Table 5.4 (Section C.3).

Comparison of the $\log_e[H(\text{likelihood})]$ values at node PIH yields $2\log_e(B_{\text{NU}}) \approx 0.15$, corresponding to no evidence for neo- over uxorilocality, $2\log_e(B_{\text{NV}}) \approx -1.36$, corresponding to no evidence for viri- over neolocality, and $2\log_e(B_{\text{UV}}) \approx -1.51$, corresponding to no evidence for viri- over uxorilocality (Table 5.4a).

Comparison of the $\log_e[H(\text{likelihood})]$ values at node PIE yields $2\log_e(B_{\text{NU}}) \approx 3.15$, corresponding to positive evidence for neo- over uxorilocality, $2\log_e(B_{\text{NV}}) \approx -4.36$, corresponding to positive evidence for viri- over neolocality, and $2\log_e(B_{\text{UV}}) \approx -7.51$, corresponding to strong evidence for viri- over uxorilocality (Table 5.4b).



(a) Prevailing mode

(b) Alternative mode

Figure 5.4: The consensus tree of Figure 4.1 for 27 IE speech varieties plus Hittite. The value above each node represents the node's posterior probability, p(node), as a percentage. Tips are colour-coded to represent the residence strategy of the corresponding society (white: N; grey: U; black: V; Hittite was not assigned residence strategy data), for (a) prevailing and (b) alternative mode. Nodes are colour-coded to represent the combined probabilities of the three states [white: $p(\mathrm{N}) \geq 0.70$; grey: $p(\mathrm{U}) \geq 0.70$; black $p(\mathrm{V}) \geq 0.70$; other nodes have combined probability < 0.70 for all states].

Table 5.3: Ancestral states of residence strategy at selected nodes on the consensus tree

(a) Prevailing mode

Node*†	p(node)	p(N|node) ± SD (range)	p(U|node) ± SD (range)	p(V|node) ± SD (range)
A	0.49	0.10 ± 0.10 (0.00–0.93)	0.05 ± 0.06 (0.00–0.50)	0.85 ± 0.15 (0.00–1.00)
B	0.78	0.10 ± 0.11 (0.00–1.00)	0.05 ± 0.06 (0.00–0.50)	0.85 ± 0.15 (0.00–1.00)
C	0.48	0.06 ± 0.06 (0.00–1.00)	0.04 ± 0.05 (0.00–0.49)	0.90 ± 0.09 (0.00–1.00)
D	0.78	0.40 ± 0.10 (0.03–1.00)	0.20 ± 0.10 (0.00–0.63)	0.40 ± 0.14 (0.00–0.89)
E	1.00	0.07 ± 0.06 (0.00–0.36)	0.05 ± 0.06 (0.00–0.50)	0.87 ± 0.10 (0.36–1.00)
F	1.00	0.05 ± 0.06 (0.00–1.00)	0.03 ± 0.04 (0.00–0.46)	0.92 ± 0.08 (0.00–1.00)

(b) Alternative mode

Node*†	p(node)	p(N|node) ± SD (range)	p(U|node) ± SD (range)	p(V|node) ± SD (range)
A	0.49	0.81 ± 0.17 (0.00–1.00)	0.13 ± 0.17 (0.00–1.00)	0.06 ± 0.06 (0.00–0.85)
B	0.78	0.86 ± 0.18 (0.00–1.00)	0.12 ± 0.18 (0.00–1.00)	0.02 ± 0.03 (0.00–0.49)
C	0.48	0.74 ± 0.11 (0.00–1.00)	0.14 ± 0.11 (0.00–1.00)	0.12 ± 0.09 (0.00–0.65)
D	0.78	0.73 ± 0.21 (0.00–1.00)	0.24 ± 0.21 (0.00–0.63)	0.03 ± 0.03 (0.00–0.42)
E	1.00	0.25 ± 0.12 (0.00–1.00)	0.26 ± 0.18 (0.00–1.00)	0.49 ± 0.24 (0.00–1.00)
F	1.00	0.94 ± 0.06 (0.45–1.00)	0.05 ± 0.06 (0.00–0.53)	0.01 ± 0.01 (0.00–0.18)

* The letters correspond to the node labels in Figure 5.4.

† The combined probabilities, p(N), p(U), and p(V), are obtained as $p(\mathrm{N}) = p(\mathrm{N}|\mathrm{node}) \cdot p(\mathrm{node})$, $p(\mathrm{U}) = p(\mathrm{U}|\mathrm{node}) \cdot p(\mathrm{node})$, and $p(\mathrm{V}) = p(\mathrm{V}|\mathrm{node}) \cdot p(\mathrm{node})$ (Section 5.2.3).

As noted in Section 5.2.3, these posterior probability distributions effectively "average" the fit of the fossil state at a node over the three sites, that is, over prevailing and alternative modes of residence; therefore, the strength of the evidence in favour of any particular state at the node is likely to be underestimated. This may partly explain the lack of evidence for any state, at least by the conservative criteria used (Section 4.2.3), at node PIH. In any case, the results broadly confirm the ancestral state estimates obtained with nodes not fossilized (Section 5.3.1.2). The lack of evidence for any state at node PIH may partly reflect the moderate skew in the posterior probability distributions of the three states at this node, for the two modes of residence (Figure 5.2). By contrast, the magnitude of the evidence for virilocality at node PIE reflects the strong skew in the posterior probability distribution towards high values for state V as prevailing mode of residence (Figure 5.3a).

5.3.3 Estimation of ancestral states at the MRCAs

At convergence, the chain sampled states in the model of trait evolution with mean $\log_e$(likelihood) $\pm$ SD $= -44.13 \pm 1.61$ (range: -56.03 to -39.84; auto-correlation coefficient: $r = 0.022$; mean acceptance rate: 28.8%; Section C.3).

Nodes CORE and EDGE reconstructed as prevailing virilocality and alternative neolocality with high posterior probabilities (Figures 5.5 and 5.6); the posterior probability distributions are qualitatively similar for the two MRCAs. This indicates that there is no evidence in the cross-cultural data, combined with the model of population history described by the linguistic data, for a shift from neo- to virilocality at node CORE. Node CORE corresponds to the ancestor of societies speaking languages in which derivatives of the reconstructed PIH affinal terms are used only for wife's in-laws; as discussed in Section 5.2.3, one of the scenarios derived from the linguistic evidence assumes a shift from neo- to virilocality at this node. Rather, the posterior probability distributions suggest that the pattern of prevailing virilocality and alternative neolocality reconstructed for PIE, and possibly for PIH, was likely maintained through to both MRCAs (Section 5.3.1.2).

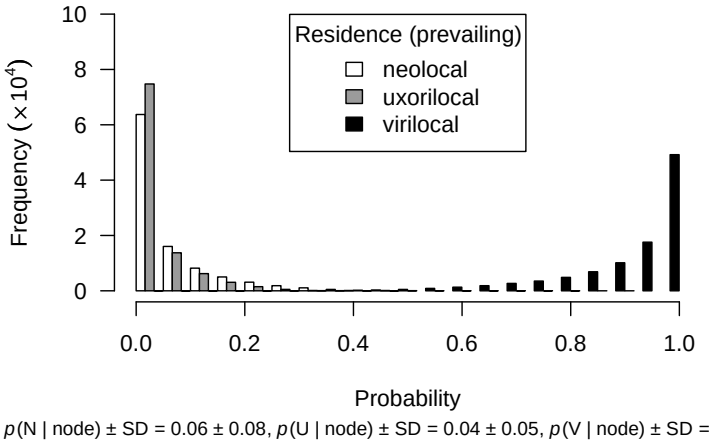
Table 5.4: Summary parameters for the samples returned by the fossilization chains

(a) Node PIH

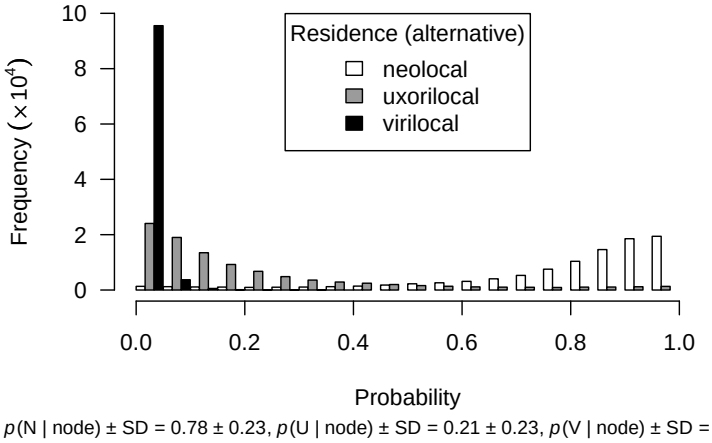
Parameter	Fossil state		
	N	U	V
Mean $\log_e$(likelihood) ± SD	-49.68 ± 1.72	-49.51 ± 1.82	-49.62 ± 1.34
Range of $\log_e$(likelihood) values	-62.25 to -45.91	-61.97 to -44.04	-61.82 to -45.98
Autocorrelation coefficient r	0.025	0.083	0.026
Mean acceptance rate	26.2%	24.7%	29.2%
$\log_e[H(\text{likelihood})]$	-52.64	-52.72	-51.96

(b) Node PIE

Parameter	Fossil state		
	N	U	V
Mean $\log_e$(likelihood) ± SD	-50.95 ± 1.89	-52.07 ± 2.34	-50.34 ± 1.51
Range of $\log_e$(likelihood) values	-64.81 to -46.26	-66.43 to -46.00	-61.60 to -45.85
Autocorrelation coefficient r	0.108	0.242	0.028
Mean acceptance rate	26.1%	16.6%	27.6%
$\log_e[H(\text{likelihood})]$	-54.70	-56.28	-52.52

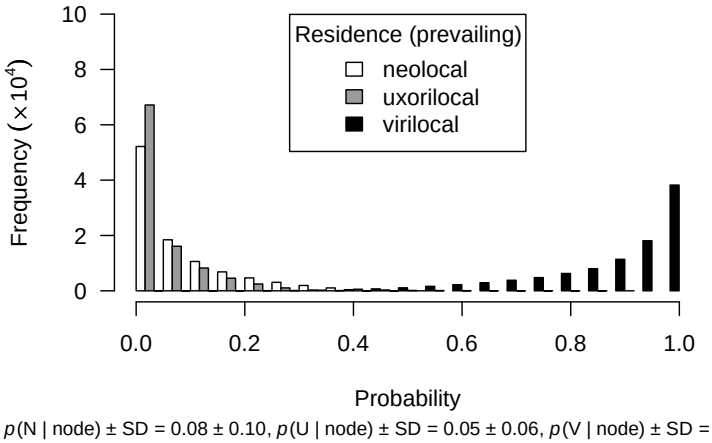


(a) Prevailing mode

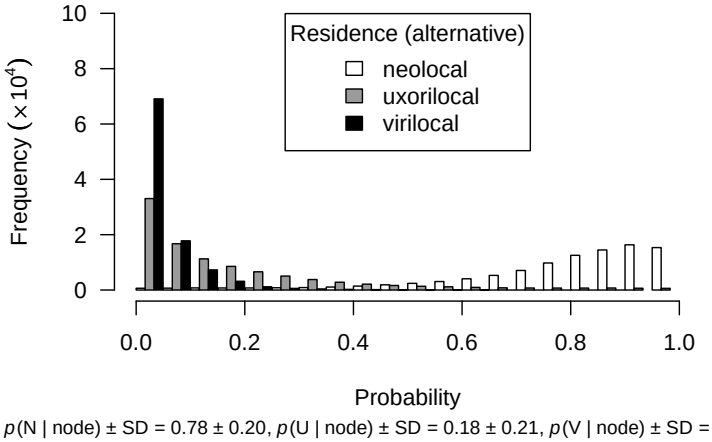


(b) Alternative mode

Figure 5.5: Posterior probability distributions of states N, U, and V at node CORE.



(a) Prevailing mode



(b) Alternative mode

Figure 5.6: Posterior probability distributions of states N, U, and V at node EDGE.

5.4 Discussion

The phylogenetic comparative analysis of residence strategies across IE-speaking societies provides evidence in support of prevailing virilocality with alternative neolocality for PIE. This pattern likely extended back to PIH, but uncertainty in the reconstructions suggests that limited confidence can be placed in inferences about PIH residence drawn from the cross-cultural data. The uncertainty may, at least in part, reflect the conflicting scenarios about this aspect of PIH social organization derived by Indo-Europeanists based on the linguistic data. One of these scenarios envisages a shift from neo- to virilocality in the ancestor of societies speaking languages that use derivatives of the reconstructed PIH affinal terms only for wife's in-laws; the present analysis finds no evidence for such a shift in the cross-cultural data. There is evidence against uxorilocality for PIE and that, throughout the history of IE-speaking societies, the acquisition of uxorilocality is more likely to have occurred through neolocality than through virilocality. These findings bolster interpretations of the archaeological evidence that emphasize the "non-matricentric" structure of early IE society; however, the finding of alternative neolocality alongside prevailing virilocality counters the notion that early IE society was strongly "patricentric".

The pattern of prevailing virilocality with alternative neolocality reconstructed for PIE and for the ancestor of societies speaking Baltic and Slavic languages concurs with the results of strontium isotope analyses of teeth recovered from burials at four prehistoric sites in Germany: three from the early Neolithic attributed to the Linear Ware culture (Bentley et al. 2002; Price et al. 2001) and one late from the late Neolithic attributed to the Corded Ware culture (Haak et al. 2008). Across these sites, the isotopic evidence yields a consistent pattern of "non-local" females and "local" males; because strontium isotope signatures in tooth enamel track the geological location of individuals during childhood, this indicates the migration of females in adult life. Assuming that the migration was linked to residential changes of females at marriage, this pattern is compatible with any system of non-uxorilocal residence (neo- or virilocality).[1] As discussed in Section 4.4, the Linear Ware and Corded

[1] *Pace* Haak et al. (2008, p. 18229), who claim that "This indicates the practice of exogamy and patrilocality". Neo- and virilocality both involve the movement of females at marriage; discrimination between these strategies requires information about the movement of males *with respect to their kin* within the community. The archaeological evidence does not provide this degree of resolution.

Ware archaeological horizons are associated with IE-speaking peoples; spanning across northern and central Europe, their range included the area later covered by Baltic and Slavic languages (Mallory 1997a,b).

High rates of female migration in the prehistory of Europe have been argued also on genetic data. Comparing geographic and genetic distances across a sample of European populations, Seielstad et al. (1998) found that genetic distance increases with geographic distance at a higher rate for the Y chromosome than for mtDNA and autosomal loci. This means that Y-chromosome variants are more clustered geographically than other genetic markers, a pattern that can be explained through the assumption of a sustained regime of virilocality in the past. However, the degree to which residence strategies operating on a local scale can explain the continent-wide pattern of migration observed by Seielstad et al. (1998) has been questioned, both on theoretical (e.g. Stoneking 1998; Wilkins and Marlowe 2006) and on empirical grounds (e.g. Kumar et al. 2006; Wilder et al. 2004). In addition to residence strategies, the genetic structuring of human populations will be affected by the permeability of marital boundaries, that is, by the pattern of endo- and exogamy across groups, and by higher-scale demographic processes associated with historical events, for example the intermarriage of in-coming males with local females, leading to the introgression of Y chromosomes but not mtDNA, typical of colonization events (Lawson Handley and Perrin 2007). Incorporating the fine-scale inferences of past residence strategies presented here into genetic analyses of sex-biased migration may help untangle these processes, and ultimately provide a better understanding of the population dynamics that shaped genetic variation in Europe.

The variability in residence strategies reconstructed for PIE and for the ancestor of societies speaking Baltic and Slavic languages, with different prevailing and alternative modes of residence, is also likely to have an effect on the observed pattern of genetic diversity. Such variability is documented early in the historical record. For example, the Hittite code of laws, which dates back to at least 1650 BCE (Bryce 2002, p. 34; Section 4.4), makes reference to cases in which the husband would take the wife "to his house", and cases in which the wife would "die in her father's house" (Bryce 2002, pp. 120–121; Hoffner 1997, pp. 181–182). The former scenario may indicate either neo- or virilocality, depending on whether a man's house corresponded to his father's; virilocality was likely if the man was his father's heir (Hoffner 1997, p. 181). The

latter scenario may refer to cases where a husband became an *antiyant-*, literally "one-entering-into (his wife's family)" (Bryce 2002, p. 124; Hoffner 1997, p. 182), and thus possibly to uxorilocality. This type of marriage was practised in the families of wealthy slave men who, through the payment of *kusata*, acquired an in-marrying son-in-law of free birth; in turn, this granted that their grandchildren were born free (Bryce 2002, pp. 123–124). More generally, its function may have been to import men into families with shortages of male members: for example, the king's daughter's husband was to become king in the absence of male heirs to the throne (Bryce 2002, pp. 28–29, 124). As discussed in Section 6.4, this variability suggests that residence strategies represent flexible social responses across descendants of PIH, and across human societies more generally.

Chapter 6

Co-evolutionary analysis of monogamy and neolocality in Indo-European-speaking societies

6.1 Introduction

6.1.1 Background

On the model developed in Chapter 2, monogamous marriage evolved as the outcome of male-female conflict over the allocation of paternity and the investment of resources, possibly coupled with ecological conditions that favoured the transfer of wealth to a limited number of heirs. By contrast, the "socially imposed monogamy" model views monogamous marriage as a mechanism of reproductive levelling, which evolved because of the benefits accrued to groups from minimizing male-male conflict over access to females (Alexander 1987, pp. 71–73; Section 2.1). In addition, monogamous marriage is argued to minimize male-female conflict over the production and rearing of offspring, especially where features of social organization limit opportunities for husbands and wives to divert resources to their respective kin. As noted in Section 5.1.1, residence strategies determine the pattern of access of individuals to kin: in this context, neolocality may have favoured the evolution of monogamous marriage by reducing the degree of differential access of husbands and wives to their own relatives (Alexander 1987, pp. 70–71). On this view, monogamous marriage represents the outcome of "complete cooperation" (Alexander 1987, p. 70) between spouses.

The association between monogamy and neolocality assumed by the "socially imposed monogamy" model largely rests on the observation that both practices prevail across societies organized in nation-states (e.g. Alexander 1987, p. 71), that is, across "the most complex of human social groups" (Alexander 1979a, p. 259; Section 4.1.1). However, ahistorical reasoning about the association between traits, based on their distribution, can easily lead to spurious inferences (Section 1.2.3), just like distributional arguments can lead to spurious inferences about the pattern of change in the traits (Sections 4.1 and 5.1).

Building on the analyses in Chapters 4 and 5, here I use the phylogenetic comparative approach to investigate the interaction between marriage and residence strategies in the history of IE-speaking societies. Indirectly, this assesses the validity of the notion of association between monogamy and neolocality, the defining features of the "nuclear family", implicit in theories that make this family type central to European social organization; as noted in Section 1.2.3.2, such theories dominate the social sciences (Goody 1996; Smith 1993).

6.1.2 Related research

To my knowledge, no formal test exists of the association between monogamous marriage and neolocal residence. Yet the potential divergence of interests between spouses in societies practising non-neolocal residence was noted as early as by Lowie (1920, p. 71), who remarked that "the rule of residence may produce a stressing of one side of the family and in so far forth interfere with the bilateral symmetry of family relations." This is because under non-neolocal residence, and in particular where marriage is exogamous with respect to the community, individuals of the dispersing sex come to rely on their spouse's kin for resources, as opposed to their own. Coupled with the fact that, by definition, non-neolocal residence results in the aggregation of individuals in extended families, this may create an asymmetry of interests between spouses (Murdock 1949, pp. 18, 202).

For example, polygyny is "particularly congenial" (Murdock 1949, p. 206) to virilocality, where men live with their relatives while their wives are isolated from their own kin: in such a system the corporate interests of related males, for instance where property is owned collectively, may increase the payoffs to husbands from investing

in their kinsmen at the expense of their wives' offspring (Murdock 1949, pp. 206–208; e.g. Goody 1970). It follows that neolocality will minimize opportunities for diverting resources to one's own relatives, by isolating both husbands and wives from their respective kin, and by preventing the formation of extended kin groups (Murdock 1949, pp. 203–204). Alexander's (1987, pp. 70–71) conjecture extends the reasoning to argue that the confluence of interest between spouses will be maximized under these conditions, leading to the co-occurrence of monogamy and neolocality across societies.

6.1.3 Rationale and objective

Previous theorizing about human family systems has assumed a functional association between monogamous marriage and neolocal residence, as these practices tend to occur together. However, the co-occurrence of traits across societies may reflect the history of the traits rather than a functional relationship between them.

Building on the ancestral state reconstructions in Chapters 4 and 5, here I use the phylogenetic comparative approach, in a Bayesian RJ-MCMC framework, to perform a co-evolutionary analysis of marriage and residence strategies in the history of IE-speaking societies. This approach provides a stringent test of presumed functional associations: two traits are taken to have co-evolved, suggestive of a functional relationship, only if they can be shown to have tended to change together throughout the history of the taxa under investigation. In other words, this approach discounts any evidence of association between traits that cannot be distinguished from associations arising from the pattern of descent of the taxa from a common ancestor.

6.2 Data and methods

Following the procedure set out in Sections 4.2 and 5.2, I used data on marriage and residence strategies from the *EA* for a sample of 27 IE-speaking societies (Section 6.2.1), mapped onto Pagel et al.'s (2007) sample of trees (Section 6.2.2). On the cross-cultural data and tree sample, I used the phylogenetic comparative method developed by Pagel and colleagues (Pagel and Meade 2005, 2006; Pagel et al. 2004) to test the hypothesis of co-evolution between monogamous marriage and neolocal residence; this method requires that the comparative data be coded in binary form (Section 6.2.3).

6.2.1 Cross-cultural data

I obtained the cross-cultural sample as described in Section 4.2.1. The data in binary form and maps of their geographical distribution are in Section B.2.

For marriage strategy, I coded societies as polygynous (state 0) or monogamous (state 1) as described in Section 4.2.1. For residence strategy, I combined the information on prevailing and alternative modes of residence, obtained as described in Section 5.2.1, into a binary variable, with societies coded as non-neolocal (state 0) or neolocal (state 1) (Section 6.2.3). Theoretically, this coding was justified on the grounds that any degree of neolocality is assumed to weaken extended family organization, even where the prevailing mode of residence is non-neolocal (Murdock 1949, p. 208).

This produced a sample with monogamy present in 15 (93.8%) of 16 neolocal societies and absent in 1 (6.2%), and with monogamy present in 3 (27.3%) of 11 non-neolocal societies and absent in 8 (72.7%) (Table B.2 and Figures B.2b and B.2e).

6.2.2 Tree sample

I obtained the tree sample as described in Section 4.2.2. The outgroup Hittite was assigned no marriage or residence strategies data for the purpose of the comparative analysis (Section 6.2.3).

6.2.3 Comparative analysis

Co-evolutionary analysis using the phylogenetic comparative method developed by Pagel and colleagues (Pagel and Meade 2005, 2006; Pagel et al. 2004) is performed using BayesDiscrete, available as part of the BayesTraits package (Pagel and Meade n.d.) from `http://www.evolution.rdg.ac.uk/BayesTraits.html`. Unless otherwise specified, the information in this section is based on Pagel and Meade (2005, 2006), Pagel et al. (2004), and on the BayesTraits manual (Pagel and Meade n.d.). I describe the method and its application in detail in Appendix C.

BayesDiscrete uses the cross-cultural data and tree sample to estimate parameters in the model of trait evolution for two binary traits (Section C.1). In this case the comparative data consisted of one trait representing the marriage strategy, with states 0 (polygynous) and 1 (monogamous), and one trait representing the residence strategy, with states 0 (non-neolocal) and 1 (neolocal) (Section 6.2.1). This produces four

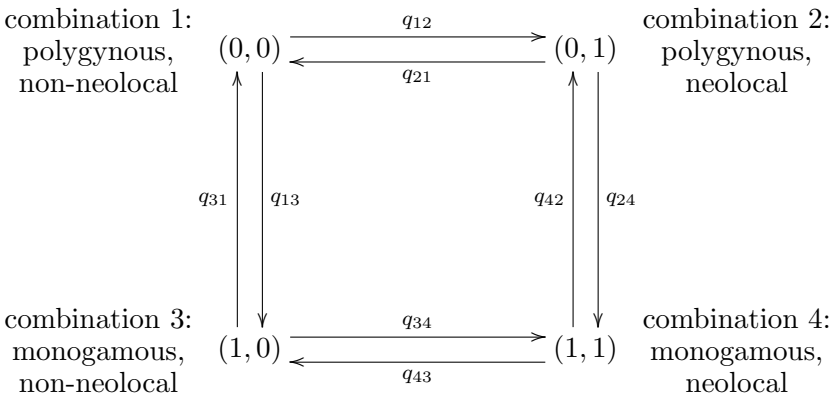


Figure 6.1: Rate parameters describing the evolution of marriage and residence strategies.

combinations of states for the two traits, as shown in Figure 6.1, e.g. combination 2 or (0, 1) for polygynous marriage with neolocal residence.

In BayesDiscrete a series of transition rate parameters q_{ij} describes the joint evolution of the two traits on a tree. These rate parameters measure the instantaneous rate of change from combination "i" to combination "j", which corresponds to the rate of change between two states of one trait while holding the state of the other trait constant. For example, rate parameter q_{12} describes transitions from combination 1 (0, 0) to combination 2 (0, 1), that is, changes from non-neolocal to neolocal residence against a background of polygynous marriage; similarly, rate parameter q_{34} describes transitions from combination 3 (1, 0) to combination 4 (1, 1), that is, changes from non-neolocal to neolocal residence against a background of monogamous marriage (Figure 6.1). Rate parameters describing simultaneous transitions in the two traits, corresponding to the diagonals of the diagram in Figure 6.1, are set to zero: this amounts to assuming that the probability of the two traits changing simultaneously is negligibly small. As in BayesMultistate (Section 4.2.3), the rate parameters are used to define the probabilities of the corresponding changes, the probabilities of the two states at internal nodes on the tree, and the likelihood of the data; taxa that are not assigned comparative data for a given trait, like the outgroup Hittite in this case (Section 6.2.2), are treated in the likelihood calculations as taking either state for the trait with equal probability.

Eight rate parameters yield 21,146 model categories, in which two or more rate parameters are set to take equal or distinct positive values; additionally, one or more

rate parameters can be set to zero. Of the 21,146 possible categories, 51 (0.24%) conform to independent trait evolution: in these categories the rate of change in one trait is not affected by the state of the other trait, that is, $q_{12} = q_{34}$, $q_{13} = q_{24}$, $q_{21} = q_{43}$, and $q_{31} = q_{42}$. All other model categories conform to dependent trait evolution, because they assign rates within one or more of these pairs to different rate classes; this means that the rate of change in one trait does depend on the state of the other trait. For example, $q_{12} = q_{34}$ specifies that the rate of change from non-neolocal to neolocal residence does not depend on whether marriage is polygynous or monogamous; $q_{12} \neq q_{34}$ indicates that it does (Figure 6.1).

Like BayesMultistate (Section 4.2.3), in Bayesian RJ-MCMC mode BayesDiscrete uses RJ-MCMC chains to produce a posterior probability sample of states in the model of trait evolution (Sections C.1 and C.2). The proportions of model categories conforming to dependent and independent evolution sampled by the chains provide a direct estimate of the posterior probability that the traits evolved dependently or independently. The theoretical prior odds is $(21,146 - 51)/51 = 413.63$: this means that if all model categories had equal posterior probability, the chains would sample categories conforming to dependent evolution approximately 414 times more frequently than categories conforming to independent evolution. The Bayes factor, obtained as the ratio of the posterior odds returned by the chains to the prior odds, provides an estimate of the posterior probability of the two evolutionary models. The Bayes factor for dependent over independent evolution is denoted B_{DI}. Values of $B_{\mathrm{DI}} > 1$ represent evidence for dependent trait evolution, values of $B_{\mathrm{DI}} < 1$ evidence for independent trait evolution. Equivalently, the Bayes factor can be expressed on a logarithmic scale, with $2\log_e(B_{\mathrm{DI}}) > 0$ representing evidence for dependent trait evolution and $2\log_e(B_{\mathrm{DI}}) < 0$ evidence for independent trait evolution. The strength of the evidence in favour of one model over the other is assessed against the scales in Table 6.1.

This implementation of the Bayes factor assumes all model categories to be equally likely, and may result in conservative estimates of support for dependent trait evolution. This is because, in practice, the processes underlying the evolution of the two traits may involve fewer than the eight transitions specified by rate parameters q_{ij}. If the "true" number of rate parameters involved in producing the observed distribution of states of the traits is less than eight, the number of possible model categories will be less than 21,146; in this case model categories conforming to independent evolution, which require

Table 6.1: Scales for interpretation of the Bayes factor*

$\lvert B_{\mathrm{DI}}\rvert$	$\lvert 2\log_e(B_{\mathrm{DI}})\rvert$	Evidence for evolutionary model
1 to 3	0 to 2	Weak
3 to 12	2 to 5	Positive
12 to 150	5 to 10	Strong
> 150	> 10	Very strong

* After Raftery (1996, p. 165).

a maximum of four distinct rate classes, will represent a higher proportion of all the possible categories, and the "true" prior odds will be lower than the theoretical value. Consequently, the posterior to prior odds Bayes factor obtained using the theoretical value of the prior odds will be lower than the "true" Bayes factor.

This issue can be circumvented through an alternative implementation of the Bayes factor. This involves running a second chain that is constrained to visit model categories conforming to independent evolution. The posterior probability distribution of $\log_e$(likelihood) values sampled by the first chain, having removed visits to model categories conforming to independent evolution, is then compared to the posterior probability distribution of $\log_e$(likelihood) values sampled by the second chain. In this case, $2\log_e(B_{\mathrm{DI}})$ is approximated as twice the difference between $\log_e[H(\text{likelihood})]$ for the first chain and $\log_e[H(\text{likelihood})]$ for the second chain, where $\log_e[H(\text{likelihood})]$ is the natural logarithm of the harmonic mean of the likelihood values. The strength of the evidence in favour of one model over the other is assessed against the logarithmic scale in Table 6.1. Because $\log_e[H(\text{likelihood})]$ may be unstable (Section 4.2.3), Pagel and Meade (n.d.) recommend taking a conservative approach, which disregards any evidence for either model given by $\lvert 2\log_e(B_{\mathrm{DI}})\rvert < 2$.

I estimated support for dependent trait evolution using both implementations of the Bayes factor. This involved running two sets of analyses: one, termed RJ-unconstrained, in which chains were free to visit all possible model categories, and one, termed RJ-constrained, in which chains were constrained to visit categories conforming to independent trait evolution. Each set of analyses comprised five separate chains started from random seeds (Section C.3). I determined the RJ-MCMC chain specifications through preliminary maximum-likelihood and MCMC runs. As for

BayesMultistate (Section 4.2.3), these specifications ensure that the RJ-MCMC chains sample parameter space adequately and ultimately converge to the posterior probability distribution of states in the model of trait evolution (Section C.3). I ran the RJ-MCMC chains for 10^8 iterations, sampling every 10^3, with an additional burn-in of 10^6, and rate deviation set to 60. Under maximum-likelihood the covarion model for trait evolution improved the mean $\log_e$(likelihood) by between 0.6 and 3.7 units, depending on the model specifications, and was therefore implemented by all RJ-MCMC chains; as noted in Section 5.2.3, this model allows rates to vary within and between branches of a tree. All chains used a uniform prior on the models and an exponential prior on the rate parameters; the mean of the exponential prior was seeded from a uniform hyperprior on the interval 0–10. The shape of the prior distribution (exponential or gamma) and the interval of the hyperprior (0–10 or 0–20) only marginally affected the mean of the posterior probability distributions of $\log_e$(likelihood) values and of ancestral states, returning qualitatively similar results.

Convergence of the chains to the target distributions and near-independence of sampling events were assessed as described in Section 4.2.3. In all cases, the diagnostics indicated that the chains sampled the target distributions adequately.

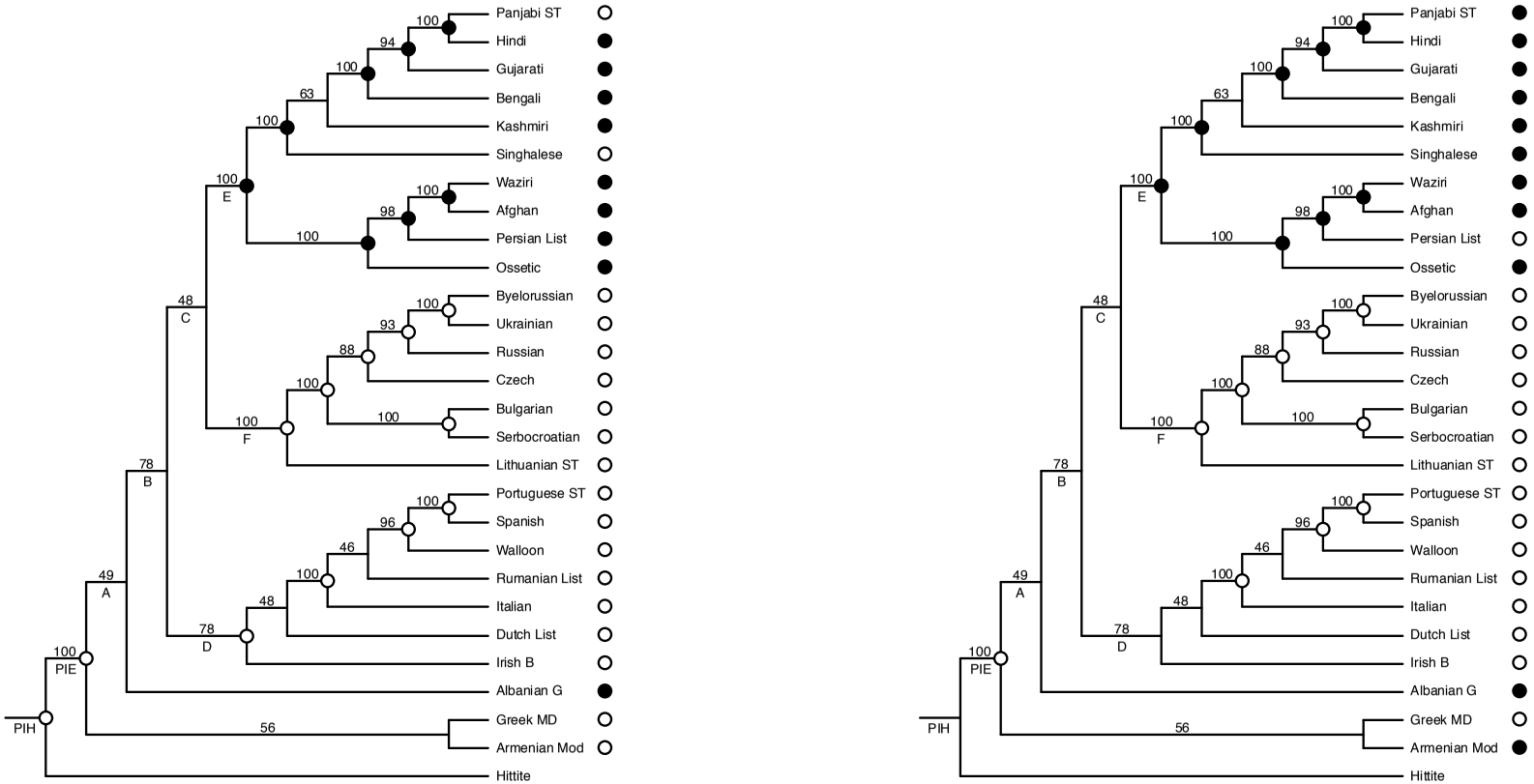
6.3 Results

For both sets of analyses, I compared the $\log_e[H(\text{likelihood})]$ values for the states in the model of trait evolution sampled by the separate chains at convergence; I present results for the chain that returned the median value of the $\log_e[H(\text{likelihood})]$.

I discuss separately the posterior probability distribution of model categories returned by the RJ-unconstrained chain (Section 6.3.1) and the estimates of support for dependent trait evolution obtained from the two implementations of the Bayes factor (Section 6.3.2). For convenience, a summary of the results of the ancestral state reconstructions from Sections 4.3.1 and 5.3.1 is in Figure 6.2.

6.3.1 Posterior probability distribution of model categories

At convergence, the RJ-unconstrained chain sampled states in the model of trait evolution with mean $\log_e$(likelihood) $\pm$ SD $= -18.86 \pm 1.34$ (range: -30.67 to -14.65; auto-correlation coefficient: $r = 0.055$; mean acceptance rate: 33.2%; Section C.3).



(a) Marriage strategy

(b) Residence strategy

Figure 6.2: The consensus tree of Figure 4.1 for 27 IE speech varieties plus Hittite. The value above each node represents the node's posterior probability, p(node), as a percentage. Tips are colour-coded to represent (a) the marriage strategy (white: monogamous; black: polygynous) and (b) the residence strategy (white: neolocal; black: non-neolocal) of the corresponding society; nodes are colour-coded to indicate that the combined probability for a state at the node is ≥ 0.70, using the same colour schemes. The residence strategy data and reconstructions were combined as non-neolocal/neolocal and over the two modes of residence (prevailing/alternative).

The chain sampled 2855 model categories, with rates assigned to 1.86±0.45 non-zero classes (mean ± SD; range: 1–4 non-zero classes). This indicates that the evolutionary processes that produced the observed distribution of states of marriage and residence strategies across societies in the sample involved fewer than the eight transitions specified by rate parameters q_{ij}. For example, the ten model categories sampled most frequently by the chain, which account for 18.2% of the 10^5 sampled points, included only one or two non-zero rate classes; these are shown in Table 6.2, together with the hundredth most frequently sampled category, which is included for comparison. The fifth most frequently sampled category sets all rates equal to each other, conforming to independent evolution, while the other nine most frequently sampled categories conform to dependent evolution.

6.3.2 Estimation of support for dependent trait evolution

Of the 10^5 points sampled by the RJ-unconstrained chain, 98.67% corresponded to model categories conforming to dependent evolution and 1.33% to categories conforming to independent evolution, yielding a posterior odds of 74.36. Comparison of the posterior to the prior odds yields $B_{DI} = 0.18$ or, on a logarithmic scale, $2\log_e(B_{DI}) = -3.43$. This corresponds to no evidence for dependent trait evolution or, equivalently, to positive evidence for independent trait evolution (Table 6.1).

Because the RJ-unconstrained chain sampled a restricted sub-set of all possible model categories, with no categories including five or more distinct non-zero rate classes, the posterior to prior odds B_{DI} may underestimate the evidence for dependent trait evolution. The alternative implementation of the Bayes factor may provide a more accurate estimate of support for dependent trait evolution. In this case, the posterior probability distribution of $\log_e$(likelihood) values sampled by the RJ-unconstrained chain, having excluded categories conforming to independent evolution (Figure 6.3a), is compared to the posterior probability distribution of $\log_e$(likelihood) values sampled by the RJ-constrained chain (Figure 6.3b). At convergence, the RJ-constrained chain sampled states with mean $\log_e$(likelihood) ± SD = −20.12 ± 0.79 (range: −27.94 to −16.37; auto-correlation coefficient: $r = 0.003$; mean acceptance rate: 35.8%; Section C.3). Comparison of the $\log_e[H(\text{likelihood})]$ values yields $2\log_e(B_{DI}) \approx 2[(-20.56) - (-20.78)] = 0.44$, and thus no evidence for dependent evolution by the conservative criteria used (Table 6.1). This reflects the substantial

Table 6.2: Rate classes and frequencies for selected model categories

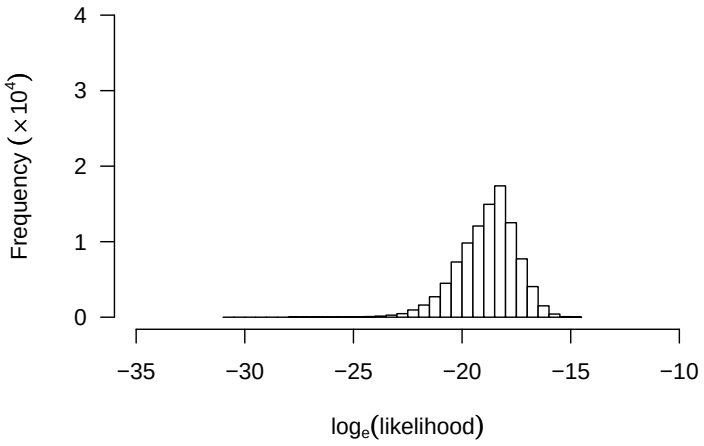
Model category	Rate class*								Frequency†	
	q_{12}	q_{13}	q_{21}	q_{24}	q_{31}	q_{34}	q_{42}	q_{43}	Absolute	Relative cumulative
1	0	0	0	Z	0	0	Z	0	5471	0.055
2	0	0	0	0	0	0	Z	0	4636	0.101
3	Z	0	0	0	0	0	0	Z	1987	0.121
4	0	1	1	Z	1	1	Z	0	1069	0.132
5	0	0	0	0	0	0	0	0	912	0.141
6	0	1	1	1	1	1	Z	0	864	0.149
7	Z	0	0	0	0	0	0	0	837	0.158
8	0	0	0	0	0	Z	0	0	832	0.166
9	0	0	0	Z	0	0	0	0	790	0.174
10	0	0	0	Z	0	0	Z	1	779	0.182
⋮										⋮
100	0	1	0	1	0	1	Z	0	242	0.531

* "Z" denotes rates assigned to the zero class. "0" and "1" denote two distinct non-zero rate classes; rates with the same value are assigned to the same non-zero rate class. For example, under model category 1 q_{12}, q_{13}, q_{21}, q_{31}, q_{34}, and q_{43} are assigned to the same non-zero rate class, that is, they take the same positive value, while q_{24} and q_{42} are assigned to the zero rate class, that is, they are set to zero.

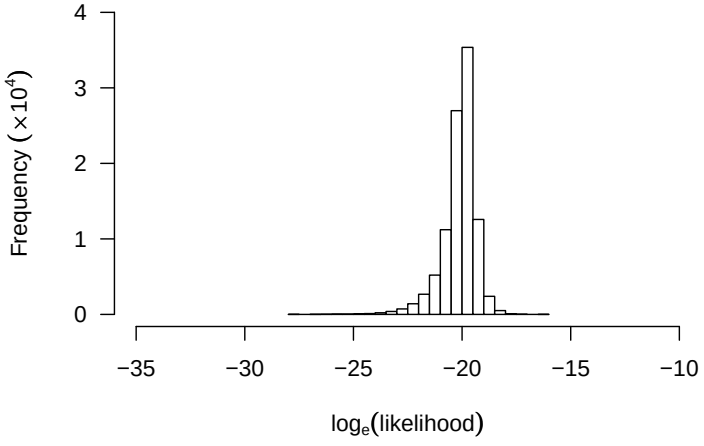
† The relative cumulative frequency of a model category is obtained by summing the absolute frequency of sampled points in the model category to the absolute frequencies of sampled points in all preceding categories, and then dividing by the total number of sampled points in all categories [e.g. $(5471 + 4636)/10^5 = 0.101$ for model category 2].

overlap in the posterior probability distributions of $\log_e$(likelihood) values sampled by the two chains (Figure 6.3).

In sum, both implementations of the Bayes factor returned no support for dependent trait evolution, indicating that there is no evidence for the hypothesis of co-evolution of monogamy and neolocality in the history of IE-speaking societies. To put these results in perspective, a non-phylogenetic analysis of the sample would return significantly higher odds of monogamous marriage for neolocal than for non-neolocal societies [odds ratio $(15/1)/(3/8) = 40.0$, $p = 0.0006$, one-tailed Fisher exact test]. This means that any evidence for correlated change in the two traits that may exist in the data



(a) Model categories conforming to dependent trait evolution



(b) Model categories conforming to independent trait evolution

Figure 6.3: Posterior probability distributions of $\log_e$(likelihood) values.

cannot be untangled from the patterning produced by the phylogenetic relationships among societies in the sample. The ancestral state reconstructions for the two traits, summarized in Figure 6.2, imply only one instance of potentially correlated change, between nodes PIE and E, leading from the presence of monogamy and neolocality in PIE to the absence of both in the ancestor of societies speaking Indo-Iranian languages (node E); a second instance is possible between node PIE and Albanian G, leading to the absence of monogamy and neolocality in the latter, but existence of the intervening node is itself uncertain (node A). In contrast, the co-occurrence of monogamy and neolocality in societies speaking Balto-Slavic languages is explained away by the presence of both practices in their ancestor (node F). Similarly, the co-occurrence of these practices in societies speaking Italic languages (Portuguese ST, Spanish, Walloon, Rumanian List, Italian) is explained away by their presence in the ancestor of the Italic sub-group; this pattern may extend back to include societies speaking Germanic and Celtic languages (Dutch List and Irish B), but phylogenetic uncertainty limits the confidence that can be placed in the reconstruction of neolocality for the ancestor of the Italic-Germanic-Celtic sub-group (node D).

6.4 Discussion

The phylogenetic comparative analysis of marriage and residence strategies across IE-speaking societies indicates that the observed association between monogamy and neolocality may be tracking the descent of societies from a common ancestor rather than a functional link between the two practices. While investigation of a larger sample may provide stronger support for the hypothesis of co-evolution, this seems unlikely given the tight clustering of marriage and residence strategies within linguistic sub-groups.

Thus, the analysis provides no evidence to support Alexander's (1987, pp. 70–71) conjecture that neolocal residence favoured the evolution of monogamous marriage by increasing the payoffs to husbands and wives from attending to their shared reproductive interests. More generally, this challenges the notion, prevalent in history and sociology of the family and in demography, of the centrality of the "isolated nuclear family" to the social organization of Europe, and of western Europe in particular (Goody 1996; Smith 1993; e.g. Hajnal 1965, 1982). Together with the reconstructions in Chapters 4 and 5, the present analysis suggests that the widespread co-occurrence in

the region of the defining elements of this family type — monogamy and neolocality — may be an artefact of descent, rather than the result of "the individualistic or nuclear tendencies of the European family system" (Smith 1993, p. 328). Consistently, the reconstructions in Chapter 5 show that neolocal residence was secondary to virilocal residence throughout the history of IE-speaking societies; by definition, virilocality results in extended family organization.

As discussed in Section 4.1.1, the emergence of monogamous marriage is typically attributed to the development of features of social organization viewed as indicators of "societal complexity" and "modernization", based on the prevalence of this marriage strategy among the "complex", "modern" societies of Eurasia. The emergence of neolocality is similarly attributed to features of social structure characteristic of "complex", "modern" societies (Levinson and Malone 1980, pp. 37–38; e.g. van den Berghe 1990, pp. 109–110): cross-cultural analyses have focused, for example, on the relationship of neolocal residence with commercialization and industrialization (e.g. de Leeuwe 1971; Ember 1967). Yet the historical evidence (discussed in Smith 1993; e.g. Laslett 1977) and the reconstructions in Chapter 5 point to an earlier origin for this residence strategy across European societies, and across IE-speaking societies more generally. Unless social and/or ecological determinants of neolocality can be identified that account for both its distribution and history, the widespread occurrence of this practice across Europe must be seen as contingent upon the nexus of descent linking societies in the region.

We currently lack a theoretical framework for understanding variation in residence strategies, both across and within societies. Theoretical work on the evolution of sex-biases in dispersal focuses on the complex interactions between (i) the costs of inbreeding, (ii) the inclusive fitness benefits of co-operating with kin, for example in the acquisition of resources (e.g. mates or food), and (iii) the inclusive fitness costs of competing with kin for those same resources (see review in Lawson Handley and Perrin 2007); extension of this framework to residence strategies may shed light on the evolutionary significance of this feature of social organization. Within this framework, various aspects of human dispersal *across* communities (that is, not necessarily in the context of residence changes at marriage) have been shown to vary in predictable ways with social and ecological factors affecting the availability of resources: for example, in agrarian societies the availability of land affects the sex of the disperser and the timing

and rate of dispersal (e.g. Beise and Voland 2008; Clarke and Low 1992; Strassmann and Clarke 1998; Towner 1999, 2001, 2002; Voland and Dunbar 1995). This suggests that in humans, as in other species, dispersal is linked to the acquisition of resources; unlike in other species, however, the acquisition of resources may be partly effected through marriage and inheritance. Across species of birds and mammals, female-biased dispersal characterizes social systems in which males compete over access to females based on their ability to defend resources critical for reproduction: in these "resource-defence" mating systems, the benefits of philopatry (e.g. familiarity with the natal territory) are greater to males than to females (Greenwood 1980). This notion has been invoked to explain female biases in dispersal in the land-based societies of Europe (e.g. Beise and Voland 2008; Clarke and Low 1992; Voland and Dunbar 1995); analogous considerations may explain the prevalence of virilocal residence throughout the history of IE-speaking societies (Chapter 5), and across human societies more generally (Koenig 1989). Sixty-four percent of societies in the *SCCS* practise prevailing virilocality (Murdock and Wilson 1972), and the incidence of this strategy is higher among societies with subsistence based on agriculture and pastoralism compared to foragers (Marlowe 2004; Wilkins and Marlowe 2006).

Intra-societal variability in residence strategies may also be explained within this framework; the reconstructions in Chapter 5 indicate that such variability likely characterized early IE society, with neolocality practised alongside virilocality in several descendants of PIE (Section 5.4). As discussed in Section 6.1.2, Alexander's (1987, pp. 70–71) hypothesis views neolocality as reducing the conflict of interests between spouses, by limiting opportunities for co-operation of spouses with their respective kin. A factor not considered by Alexander (1987) is that, at the same time, neolocality limits opportunities for competition of spouses with their kin; competition between relatives can alter the evolutionary dynamics in important ways, even to the point of negating the effect of kin selection for co-operation where local competition is intense (West et al. 2002). Crucially, the relative costs and benefits of foregoing co-operation and avoiding competition with kin will depend on other aspects of social organization besides the marriage strategy itself, notably the pattern of marital endo- and exogamy across groups, and the ability of individuals within groups to monopolize reproductive opportunities (i.e. the degree of reproductive skew; Emlen 1995, 1997). Recent developments in the theory of social evolution stress the need to focus on the

net effect of co-operation and competition between relatives in the study of social interactions (see review in West et al. 2007a); incorporating these developments into the analysis of kinship and marriage systems holds great promise for furthering our understanding of the evolution of human social behaviour.

Chapter 7

Conclusion

The work presented in this thesis contributes to the development of what Hughes (1988, p. 21) envisioned as "a biologically based social anthropology." It is "biologically based" in that it is grounded in evolutionary biology; it constitutes "social anthropology" because its concern is the study of the social systems of the human species. The general themes that emerge from this work represent the substantive contributions of the thesis to the study of kinship and marriage systems.

The theoretical analysis in Chapter 2 shows that the practice of monogamous marriage can be understood within the framework of inclusive fitness theory. This result challenges previous explanations for the evolution of monogamous marriage, and explanations for the evolution of marriage strategies more generally: the former assume the implication of group-level processes, while both assume that male reproductive success is always maximized by polygynous marriage or, equivalently, that variance in male reproductive success is always greater under polygynous than under monogamous marriage. The framework developed in Chapter 2 makes both assumptions unnecessary. Rather, it shows that where resources are transferred across generations and are linked to fitness, whether monogamous or polygynous marriage represents the optimal strategy for males depends on whether the value of resources is depleted through division among multiple heirs; some form of division is inevitable if multiple wives are involved.

The excessive focus on variance in male reproductive success as the prime determinant of male-female interactions, and the consequent neglect of female behaviour, is evident also in evolutionary explanations for variation in transfer strategies. These rely on the notion that natural selection will favour males who allocate resources

strategically, based on their level of paternity (e.g. Alexander 1974; Greene 1978; Kurland 1979). The analysis in Chapter 2 extends this paradigm to incorporate the strategic behaviour of females: if selection favours males who allocate resources strategically, based on their level of paternity, it is also likely to favour females who allocate paternity strategically, based on the level of male investment in their offspring. This simple extension has important implications for analysis of the evolution of marriage strategies, leading to a situation where both males and females stand to gain from monogamous marriage: males benefit from investing resources "safely" in the individuals in the next generation that provide the greatest potential fitness returns, that is, their wife's offspring; females, in turn, benefit from exclusive investment of their husband's resources in their own offspring. In a similar way, this extension is likely to have important implications for analysis of the evolution of other aspects of social organization that are linked to transfer strategies: for example, the notion of strategic male behaviour in this context underlies current explanations for the evolution of descent systems (see review in Cronk and Gerkey 2007).

In testing hypotheses about of the evolution of marriage strategies, previous cross-cultural analyses have relied heavily on the bias in focus towards male behaviour — what Hrdy and Williams (1983) term the "double standard" of behavioural biology (see Clutton-Brock 2007 for a more general discussion). Typically, the degree of polygyny captured by a society's marriage strategy has been used as a proxy for mating strategy or, equivalently, for variance in male reproductive success (Low 1988); this may explain why cross-cultural studies have generally failed to identify clear social or ecological correlates of monogamous marriage (see review in Low 2003, 2007). By contrast, the cross-cultural analysis in Chapter 3 does not assume that monogamous marriage involves monogamous mating, thus keeping distinct the "social" category of marriage from the "biological" category of mating. The pattern identified by the analysis in Chapter 3 provides support for the association between monogamous marriage and the transfer of property to wife's offspring predicted by the theoretical analysis in Chapter 2.

The analyses in Chapters 2 and 3 provide a robust framework for interpretation of the evidence — archaeological, historical, and ethnographic — on the emergence and cross-cultural distribution of monogamous marriage. Crucially, by situating variation in marriage strategies in the context of variation in ecological factors, this framework is compatible with a relatively early historical origin of monogamy; in this fundamental

respect it contrasts with evolutionary and non-evolutionary explanations that, implicitly or explicitly, link the emergence of monogamous marriage to the development of markers of "societal complexity" and "modernization", or to "societal complexity" and "modernization" *per se*. In contrast to these explanations, but in line with the framework developed in Chapters 2 and 3, the cross-cultural analysis in Chapter 4 reconstructs a prehistoric origin for monogamous marriage in societies speaking Indo-European languages. Further, the cross-cultural analysis in Chapter 6 shows that, across these societies, the observed association between monogamous marriage and neolocal residence may be the artefact of a history of descent from a common ancestor; neolocality is itself viewed as a marker of "societal complexity" and "modernization". Consistently, the cross-cultural analysis in Chapter 5 reconstructs a prehistoric origin for neolocality, albeit secondary to virilocality, in Indo-European-speaking societies.

Together, the reconstructed histories of the two defining features of the "nuclear family", monogamy and neolocality, challenge theoretical claims to the centrality of this family type to European and, more generally, to "western" social organization. In turn, this challenges explanations that ascribe the "nuclear tendencies" of the European family to the influence of Christian ideology on kinship and marriage systems (Smith 1993). The cross-cultural analysis in Chapter 3 provides empirical evidence in support of the association between monogamous marriage and Christianization assumed by these explanations; at the same time, however, it shows that the relationship between monogamous marriage and transfer of land to wife's offspring is not confounded with the interaction of marriage strategy with religious affiliation. In line with the available evidence on the history and diffusion of Christianity, this suggests that the standard "cultural infection" scenario, whereby monogamous marriage spread "passively" alongside Christianity, is too simplistic. The available evidence is, at present, anecdotal; quantitative historical and ethnographic data will be required to formally evaluate the alternative pathways that may have produced the observed association between monogamous marriage and Christianization. This will constitute an important test of widely-held assumptions about the history of kinship and marriage systems and, more generally, about the interactions between micro- and macro-evolutionary processes that shaped the observed pattern of cultural variation (Borgerhoff Mulder et al. 2006).

Finally, together with previous analyses (Fortunato et al. 2006; Fortunato and Mace 2009), the reconstructions of early Indo-European social organization in Chapters 4

and 5 point to a society practising monogamy, virilocality with neolocality, and dowry. On the ethnographic evidence, this type of social structure is compatible with interpretations of the linguistic evidence that attribute to Indo-European society an economy based on domesticated plants and animals, with use of the plough, a settled lifestyle, and possibly some form of social ranking based on social status differentiation (Mallory and Adams 2006, p. 284). The reconstructions seem harder to reconcile with interpretations of the linguistic evidence that tend to emphasize elements pointing to a pastoral economy and nomadic lifestyle; these interpretations provide the basis for the traditional view that Indo-European languages propagated across Eurasia with warlike nomadic pastoralists (e.g. Anthony 2007; Gimbutas 1991; Mallory 1989), but are being criticized also on linguistic grounds (e.g. Krell 1998). In fact, the traditional view has strongly influenced reconstructions of other aspects of early Indo-European social life; in turn, these reconstructions have been used to substantiate the traditional view of Indo-European origin (Renfrew 1987, pp. 260–262). The analyses in Chapters 4 and 5 avoid this circularity because the inferences are derived entirely from the cross-cultural data, in conjunction with the model of population history captured by the linguistic evidence; consequently, the inferential process is relatively assumption-free with regards to early Indo-European social organization. One implicit assumption is that practices observed in the "ethnographic present" can be used to characterize early Indo-European social structure. The analytical categories used in Chapters 4 and 5 are based on the simplest possible conceptualization of marriage and residence strategies; as such, they apply to the range of social systems found in the ethnographic record. They are therefore likely to apply also to the range of social systems involved in the history of dispersal of Indo-European-speaking societies from a common ancestor.

Overall, the findings in Chapters 3 to 6 emphasize the importance of using systematic and, where possible, explicitly historical approaches to cross-cultural comparison. The formulation of analytical categories that are theoretically justifiable and empirically useful is one of many advances that derive from extension of the philosophical, theoretical, and methodological foundations of evolutionary biology to the study of kinship and marriage systems. More generally, placing variation in human social systems in the wider context of variation in animal social systems offers a unique opportunity for progressing the analysis of human behaviour beyond debates about whether or not our species evolved "by genes alone" (e.g. Richerson and Boyd 2005).

These debates are trite, futile, and easily dismissed: they stem from confusion of the ultimate and proximate levels of explanation or, more prosaically, from not keeping clearly in mind that genes are segments of nucleic acid that direct the synthesis of amino acids (Turke 1984). At the ultimate level of analysis considered in this thesis there is no evidence to show, nor any reason to assume, that the "biological" paradigm is less suited to explaining human behaviour than it is to explaining the behaviour of other species. On this premise, any distinctly human features are viewed as part of the repertoire of species-specific proximate mechanisms through which the "biological" paradigm is effected; with regards to kinship and marriage systems, these include the use of linguistic and symbolic categories to conceptualize behaviours linked to relatedness and reproduction, and to encode these behaviours in social norms. Only within the wider context of variation in animal social behaviour it becomes apparent that distinctive species-specific traits exist, by definition, in any species: this represents the very principle upon which taxonomic classification of the living world is based! In contrast, too narrow a focus on proximate mechanisms when searching for evolutionary explanations generates the impression that the species under investigation is somehow "special" — an impression that is used to justify the assumption that the species' behaviour can only be explained through "special" ultimate causes. While this may be a legitimate conclusion that cannot be excluded *a priori*, it is not a legitimate starting point in a sound scientific framework: by taking this proposition as a given at the outset, one renounces the possibility to demonstrate it.

Put differently, the pervasiveness of socially transmitted behaviour in our species does not invalidate application of the "biological" paradigm to the analysis of human social systems, nor does it validate the claim that "culture transformed human evolution" (e.g. Richerson and Boyd 2005). Whether the predisposition for cultural behaviour in humans is indeed unique, in degree if not in kind, and how genetic and cultural processes interacted to shape human evolution are important questions; substituting these questions for questions about the survival value of human behaviour is an egregious mistake.

A "mature science of society" will comprise general principles applicable to any species, and specific principles applicable to individual taxonomic groups (Hughes 1988, p. 141); together, they will need to account for the ultimate causes of behaviour and for its proximate determinants, as well as for the interactions between genetic and cultural

processes in *any* species with social transmission (Rogers 1988). Given the emphasis on cultural evolution in the study of human behaviour (e.g. Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1981), this will likely involve "a mutual transformation" of biology and anthropology (Wilson 1979). This, in turn, will represent an indispensable step towards integration of evolutionary approaches to the analysis of human behaviour (reviewed in Laland and Brown 2002), culminating in the development of a biologically based social anthropology.

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Appendix A

Inclusive fitness analysis

A.1 Theoretical framework

A.1.1 Male and female strategies

We consider a population with n males and n females, in which individuals marry either monogamously (M) or polygamously (P). We use $w \geq 1$ to denote the number of wives for males and $h \geq 1$ the number of husbands for females; males and females marry with probabilities Ω and Φ, respectively, which are derived in Section A.1.2.

Each female produces one male and one female offspring. Unmarried females transfer their resources, denoted δ_{f}, to their own offspring, whereas unmarried males transfer their resources, denoted δ_{m}, to their sister's offspring. The resources of married females are controlled by their husbands, i.e. a male controls his own δ_{m} and a share $1/h$ of the δ_{f} of each of his w wives. Males transfer resources "vertically" to their wife's (or wives') offspring (V), with probability m_{V}, or "diagonally" to their sister's offspring (D), with probability m_{D}; each male transfers either vertically or diagonally, i.e. m_{V} and m_{D} take values 0 or 1, and $m_{\mathrm{V}} = 1 - m_{\mathrm{D}}$. To simplify the notation, we assume that individuals in the parent generation transfer resources to sibling pairs rather than to individuals in the offspring generation. Each sibling pair inherits resources δ, with $\delta = \delta_{\mathrm{m}} + \delta_{\mathrm{f}} = 1$ for the offspring of a monogamous couple in a monogamous population in which all males transfer vertically. The fitness of each sibling pair is given by δ^z, with $z > 0$. $\delta_{\mathbb{B}'}$ and $\delta_{\mathbb{F}'}$ denote the resources inherited by sibling pairs $\mathbb{B}'$ and $\mathbb{F}'$, respectively (Figure 2.1).

The probability p that a male is the biological father of his wife's offspring depends on the behaviour of females. Females give their husbands either "high" paternity p_{H} (H) or "low" paternity p_{L} (L), with $0 < p_{\mathrm{L}} < p_{\mathrm{H}} \leq 1$. Females obtain an additional generic advantage α from mating with other males besides their husbands; for example, α may represent genetic benefits which lead to increased offspring survival or resource benefits such as nuptial gifts (Kokko 1999; Reynolds 1996). We assume that $\alpha_{\mathrm{L}} > \alpha_{\mathrm{H}}$, and $\alpha_{\mathrm{H}} = 0$ for $p_{\mathrm{H}} = 1$. For simplicity, we further assume that $0 < \alpha < 1/2$, such that its fitness value is small relative to the value of the resources transferred to the offspring generation, and does not affect the amount of resources males transfer to their wives' or sister's offspring.

Both males and females know their spouses' marriage strategy. The transfer strategy of males may be conditional upon the marriage and paternity strategies of females. A "suspicious" male (S) transfers vertically if his wives are monogamous and provide paternity p_{H}, diagonally otherwise. An "ingenuous" male (I) transfers diagonally if his wives are monogamous and provide paternity p_{H}, vertically otherwise. These strategies require that males have cues about paternity (e.g. Kokko 1999): in humans, these include direct phenotypic cues or indirect behavioural cues (e.g. the conformity of females to cultural norms regulating their sexual behaviour). The paternity strategy of females may be conditional only upon the marriage strategy of males. An "astute" female (A) provides paternity p_{H} if her husbands marry monogamously, p_{L} otherwise. A "naive" female (N) provides paternity p_{L} if her husbands marry monogamously, p_{H} otherwise.

Table A.1 presents a summary of the strategies included in the game. We use XY to denote the marriage strategy X and transfer strategy Y for a male, XZ to denote the marriage strategy X and paternity strategy Z for a female, and (XY, XZ) to denote a pair of male and female strategies. For example, (MV, MH) represents the interaction of a monogamous male who transfers vertically, MV, with a monogamous female who always provides "high" paternity, MH. Table A.2 presents a summary of all the symbols used in the model.

A.1.2 Marriage probabilities

For simplicity, we assume that polygamous individuals either marry w or h spouses, or do not marry at all. Denoting m_{M} and m_{P} the frequencies of monogamous and

Table A.1: Summary of the strategies included in the game

(a) Male strategies

Strategy			Description
Attribute	Symbol	Behaviour	
Marriage (X)	M	Monogamous	Male marries one female only ($w = 1$)
	P	Polygynous	Male marries more than one female ($w > 1$)
Transfer (Y)	V	Vertical	Married male transfers resources to wives' offspring
	D	Diagonal	Married male transfers resources to sister's offspring
	S	Suspicious	Married male is V if wife is M and provides p_{H}, D otherwise
	I	Ingenuous	Married male is D if wife is M and provides p_{H}, V otherwise

(b) Female strategies

Strategy			Description
Attribute	Symbol	Behaviour	
Marriage (X)	M	Monogamous	Female marries one male only ($h = 1$)
	P	Polyandrous	Female marries more than one male ($h > 1$)
Paternity (Z)	H	High	Married female provides "high" paternity ($0 < p_{\mathrm{H}} \leq 1$, α_{H})
	L	Low	Married female provides "low" paternity ($0 < p_{\mathrm{L}} < 1$, α_{L})
	A	Astute	Married female provides p_{H} if husband is M, p_{L} otherwise
	N	Naive	Married female provides p_{L} if husband is M, p_{H} otherwise

Table A.2: Symbols used in the model

Notation	Description
X	marriage strategy (of males and females); can be M, P (Table A.1)
Y	transfer strategy (of males); can be V, D, S, I (Table A.1a)
Z	paternity strategy (of females); can be H, L, A, N (Table A.1b)
n	number of individuals of each sex in the population
Ω, Φ	marriage probability for a male and for a female
m_{M}, m_{P}	frequency of monogamous and of polygynous males in the population
f_{M}, f_{P}	frequency of monogamous and of polyandrous females in the population
w, w_{P}	number of wives for a male (generic and for a polygynous male)
h	number of husbands for a female (generic)
δ, $\delta_{\mathbb{B}'}$, $\delta_{\mathbb{F}'}$	resources inherited by a sibling pair in the offspring generation (generic, by sibling pair $\mathbb{B}'$, and by sibling pair $\mathbb{F}'$) (Figure 2.1)
δ_{m}, δ_{f}	relative male and female contribution to δ
z	describes the relationship between inherited resources and fitness, given by δ^z
m_{V}, m_{D}	probability that a male transfers vertically and diagonally
p, p_{H}, p_{L}	probability that a female's husband is the biological father of her offspring (generic, for a female who provides "high" paternity, and for a female who provides "low" paternity)
α, α_{H}, α_{L}	advantage to a female of mating with other males besides her husbands (generic, for a female who provides "high" paternity, and for a female who provides "low" paternity)
$\mathbb{M}$, $\mathbb{F}$	focal male and female (or sibling to the focal individual) (Figure 2.1)
$\mathbb{A}$	$\mathbb{F}$'s husband
$\mathbb{B}$	$\mathbb{M}$'s wife
$\mathbb{C}$	$\mathbb{B}$'s brother
$\mathbb{B}'$	$\mathbb{B}$'s offspring
$\mathbb{F}'$	$\mathbb{F}$'s offspring
$E_{\mathbb{M}}$, $E_{\mathbb{F}}$	inclusive fitness for a focal male and for a focal female
β_i, ϕ_i	resources transferred to $\mathbb{B}'$ and to $\mathbb{F}'$ (Figure 2.1)
r_{xy}	coefficient of relatedness of focal individual x ($\mathbb{M}$ or $\mathbb{F}$) to heir y ($\mathbb{B}'$ or $\mathbb{F}'$)
$^\circ$	denotes any attribute that may depend on the relevant strategy for the focal individual

polygynous males in the population, and f_{M} and f_{P} the frequencies of monogamous and polyandrous females, a focal monogamous male marries with probability

$$\Omega_{\mathrm{M}} = \begin{cases} f_{\mathrm{M}}\left[m_{\mathrm{M}} \cdot 1 + m_{\mathrm{P}} \dfrac{n}{(n-1)w+1}\right] + f_{\mathrm{P}}\left[m_{\mathrm{M}} \cdot 1 + m_{\mathrm{P}} \dfrac{nh}{(n-1)w+1}\right] \\ \qquad\qquad \text{if} \quad \dfrac{nh}{(n-1)w+1} \leq 1 \\ f_{\mathrm{M}}\left[m_{\mathrm{M}} \cdot 1 + m_{\mathrm{P}} \dfrac{n}{(n-1)w+1}\right] + f_{\mathrm{P}}[m_{\mathrm{M}} \cdot 1 + m_{\mathrm{P}} \cdot 1] \\ \qquad\qquad \text{if} \quad \dfrac{nh}{(n-1)w+1} \geq 1 \end{cases}.$$

This is derived as follows:

- in a population of monogamous females and monogamous males there are n females, each requiring one husband, and n males, each requiring one wife; thus, the focal male marries with probability $\Omega_{\mathrm{M}} = 1$;
- in a population of monogamous females and polygynous males there are n females, each requiring one husband, $n-1$ resident polygynous males, each requiring w wives, and the focal monogamous male, requiring one wife; thus, the focal male marries with probability $\Omega_{\mathrm{M}} = n/[(n-1)w+1]$;
- in a population of polyandrous females and monogamous males there are n females, each requiring h husbands, and n males, each requiring one wife; thus, the focal male marries with probability $\Omega_{\mathrm{M}} = 1$;
- in a population of polyandrous females and polygynous males there are n females, each requiring h husbands, $n-1$ resident polygynous males, each requiring w wives, and the focal monogamous male, requiring one wife; thus, the focal male marries with probability $\Omega_{\mathrm{M}} = nh/[(n-1)w+1]$ if the number of potential wives is smaller than the number of wives required, i.e. if $nh/[(n-1)w+1] \leq 1$, or with probability $\Omega_{\mathrm{M}} = 1$ if the number of potential wives is greater than the number of wives required, i.e. if $nh/[(n-1)w+1] \geq 1$.

By similar reasoning, a focal polygynous male marries with probability

$$\Omega_{\mathrm{P}} = \begin{cases} f_{\mathrm{M}}\left[m_{\mathrm{M}}\dfrac{n}{(n-1)+w} + m_{\mathrm{P}}\dfrac{1}{w}\right] + f_{\mathrm{P}}\left[m_{\mathrm{M}}\cdot 1 + m_{\mathrm{P}}\dfrac{h}{w}\right] & \text{if} \quad \dfrac{h}{w} \leq 1 \\ f_{\mathrm{M}}\left[m_{\mathrm{M}}\dfrac{n}{(n-1)+w} + m_{\mathrm{P}}\dfrac{1}{w}\right] + f_{\mathrm{P}}\left[m_{\mathrm{M}}\cdot 1 + m_{\mathrm{P}}\cdot 1\right] & \text{if} \quad \dfrac{h}{w} \geq 1 \end{cases}.$$

Assuming that n is large relative to h and w, Ω_{M} and Ω_{P} simplify to

$$\Omega = \begin{cases} f_{\mathrm{M}}\left(m_{\mathrm{M}}\cdot 1 + m_{\mathrm{P}}\dfrac{1}{w}\right) + f_{\mathrm{P}}\left(m_{\mathrm{M}}\cdot 1 + m_{\mathrm{P}}\dfrac{h}{w}\right) & \text{if} \quad \dfrac{h}{w} \leq 1 \\ f_{\mathrm{M}}\left(m_{\mathrm{M}}\cdot 1 + m_{\mathrm{P}}\dfrac{1}{w}\right) + f_{\mathrm{P}}\left(m_{\mathrm{M}}\cdot 1 + m_{\mathrm{P}}\cdot 1\right) & \text{if} \quad \dfrac{h}{w} \geq 1 \end{cases},$$

which, assuming that $h = w$, simplifies to

$$\Omega = f_{\mathrm{M}}\left(m_{\mathrm{M}} + \frac{m_{\mathrm{P}}}{w}\right) + f_{\mathrm{P}}.$$

The probability of marrying for females is derived by analogous reasoning. Assuming that n is large relative to h and w, a focal female marries with probability

$$\Phi = \begin{cases} m_{\mathrm{M}}\left(f_{\mathrm{M}}\cdot 1 + f_{\mathrm{P}}\dfrac{1}{h}\right) + m_{\mathrm{P}}\left(f_{\mathrm{M}}\cdot 1 + f_{\mathrm{P}}\dfrac{w}{h}\right) & \text{if} \quad \dfrac{w}{h} \leq 1 \\ m_{\mathrm{M}}\left(f_{\mathrm{M}}\cdot 1 + f_{\mathrm{P}}\dfrac{1}{h}\right) + m_{\mathrm{P}}\left(f_{\mathrm{M}}\cdot 1 + f_{\mathrm{P}}\cdot 1\right) & \text{if} \quad \dfrac{w}{h} \geq 1 \end{cases},$$

which, assuming that $h = w$, simplifies to

$$\Phi = m_{\mathrm{M}}\left(f_{\mathrm{M}} + \frac{f_{\mathrm{P}}}{h}\right) + m_{\mathrm{P}}.$$

A.1.3 Inclusive fitness payoffs

We use $\mathring{}$ to indicate any attribute that may depend on the relevant strategy for the focal individual, such that its value may differ from the corresponding value for the resident population. For example, $\mathring{w} \geq 1$ denotes the number of wives for a focal male $\mathbb{M}$, with $\mathring{w} \neq w$ for a mutant focal male whose marriage strategy differs from the strategy of resident males, and $\mathring{w} = w$ in all other cases. With reference to Figure 2.1, the inclusive

fitness payoff for a focal male $\mathbb{M}$ can be written as

$$
\begin{aligned}
E_{\mathbb{M}} \;=\; & \mathring{w}\Bigg\{\Bigg[\underbrace{\Omega\,\mathring{m}_{\mathrm{V}}\left(\delta_{\mathrm{m}}+\mathring{w}\,\frac{\delta_{\mathrm{f}}}{h}\right)}_{\beta_1}+\underbrace{\Omega\,\mathring{w}\,m_{\mathrm{V}}(h-1)\left(\frac{\delta_{\mathrm{m}}}{w}+\frac{\delta_{\mathrm{f}}}{h}\right)}_{\beta_2} \\
& +\underbrace{\Omega\,\mathring{w}\,(1-\Omega)\delta_{\mathrm{m}}}_{\beta_3}+\underbrace{\Omega\,\mathring{w}\,\Omega\,m_{\mathrm{D}}\left(\delta_{\mathrm{m}}+w\,\frac{\delta_{\mathrm{f}}}{h}\right)}_{\beta_4}\Bigg]/\mathring{w}\Bigg\}^{z} r_{\mathbb{MB}'} \\
& +\Bigg[\underbrace{(1-\Omega)\delta_{\mathrm{m}}}_{\phi_1}+\underbrace{\Omega\,\mathring{m}_{\mathrm{D}}\left(\delta_{\mathrm{m}}+\mathring{w}\,\frac{\delta_{\mathrm{f}}}{h}\right)}_{\phi_2}+\underbrace{(1-\Phi)\delta_{\mathrm{f}}}_{\phi_3}+\underbrace{\Phi\,h\,m_{\mathrm{V}}\left(\frac{\delta_{\mathrm{m}}}{w}+\frac{\delta_{\mathrm{f}}}{h}\right)}_{\phi_4}\Bigg]^{z} r_{\mathbb{MF}'},
\end{aligned}
$$

where β_i represents resources inherited by the offspring $\mathbb{B}'$ of his $\mathring{w}$ wives and ϕ_i represents resources inherited by his sister's offspring $\mathbb{F}'$; the subscript $i = 1, \ldots, 4$ denotes the pathway through which resources are transferred to the heir. $r_{\mathbb{MB}'}$ and $r_{\mathbb{MF}'}$ represent the coefficients of relatedness between $\mathbb{M}$ and, respectively, $\mathbb{B}'$ and $\mathbb{F}'$, as derived in Section A.1.4.

β_1, β_2, β_3, and β_4 are only relevant if $\mathbb{M}$ marries, while ϕ_4 is only relevant if $\mathbb{F}$ marries. Specifically:

- β_1 represents the resources $\mathbb{M}$ transfers to $\mathbb{B}'$ if his transfer strategy is V; this includes his δ_{m} and a share $1/h$ of the δ_{f} of each $\mathbb{B}$;
- β_2 represents the resources transferred to $\mathbb{B}'$ by the other $h-1$ husbands of each $\mathbb{B}$, excluding $\mathbb{M}$, if the transfer strategy of resident males is V; for each husband, this includes a share $1/w$ of his δ_{m} and a share $1/h$ of $\mathbb{B}$'s δ_{f};
- β_3 represents the resources each $\mathbb{C}$ transfers to $\mathbb{B}'$ if he does not marry;
- β_4 represents the resources each $\mathbb{C}$ transfers to $\mathbb{B}'$ if he marries and his transfer strategy is D; this includes his δ_{m} and a share $1/h$ of the δ_{f} of each of his w wives;
- ϕ_1 represents the resources $\mathbb{M}$ transfers to $\mathbb{F}'$ if he does not marry;
- ϕ_2 represents the resources $\mathbb{M}$ transfers to $\mathbb{F}'$ if he marries and his transfer strategy is D; this includes his δ_{m} and a share $1/h$ of the δ_{f} of each $\mathbb{B}$;
- ϕ_3 represents the resources $\mathbb{F}$ transfers to $\mathbb{F}'$ if she does not marry;

ϕ_4 represents the resources each $\mathbb{A}$ transfers to $\mathbb{F}'$ if the transfer strategy of resident males is V; this includes a share $1/w$ of his δ_{m} and a share $1/h$ of $\mathbb{F}$'s δ_{f}.

The inclusive fitness payoff for a focal female $\mathbb{F}$ is derived by analogous reasoning, and can be written as

$$\begin{aligned} E_{\mathbb{F}} \;=\; & w\Bigg\{\Bigg[\underbrace{\Omega\, m_{\mathrm{V}}\left(\delta_{\mathrm{m}} + w\,\frac{\delta_{\mathrm{f}}}{h}\right)}_{\beta_1} + \underbrace{\Omega\, w\, m_{\mathrm{V}}(h-1)\left(\frac{\delta_{\mathrm{m}}}{w} + \frac{\delta_{\mathrm{f}}}{h}\right)}_{\beta_2} \\ & + \underbrace{\Omega\, w\,(1-\Omega)\delta_{\mathrm{m}}}_{\beta_3} + \underbrace{\Omega\, w\, \Omega\, m_{\mathrm{D}}\left(\delta_{\mathrm{m}} + w\,\frac{\delta_{\mathrm{f}}}{h}\right)}_{\beta_4}\Bigg]/w\Bigg\}^{z} r_{\mathbb{F}\mathbb{B}'} \\ & + \Bigg[\underbrace{(1-\Omega)\delta_{\mathrm{m}}}_{\phi_1} + \underbrace{\Omega\, m_{\mathrm{D}}\left(\delta_{\mathrm{m}} + w\,\frac{\delta_{\mathrm{f}}}{h}\right)}_{\phi_2} + \underbrace{(1-\Phi)\delta_{\mathrm{f}}}_{\phi_3} + \underbrace{\Phi\, \mathring{h}\, \mathring{m}_{\mathrm{V}}\left(\frac{\delta_{\mathrm{m}}}{w} + \frac{\delta_{\mathrm{f}}}{\mathring{h}}\right)}_{\phi_4}\Bigg]^{z} r_{\mathbb{F}\mathbb{F}'} + \mathring{\alpha}, \end{aligned}$$

where β_i represents resources inherited by the offspring $\mathbb{B}'$ of her brother's w wives and ϕ_i represents resources inherited by her offspring $\mathbb{F}'$; as in the previous case, the subscript $i = 1, \ldots, 4$ denotes the pathway through which resources are transferred to the heir. $r_{\mathbb{F}\mathbb{B}'}$ and $r_{\mathbb{F}\mathbb{F}'}$ represent the coefficients of relatedness between $\mathbb{F}$ and, respectively, $\mathbb{B}'$ and $\mathbb{F}'$, as derived in Section A.1.4. $\mathring{\alpha} \neq \alpha$ for a mutant focal female whose paternity strategy differs from the strategy of resident females, and $\mathring{\alpha} = \alpha$ in all other cases.

As in the previous case, β_1, β_2, β_3, and β_4 are only relevant if $\mathbb{M}$ marries, while ϕ_4 is only relevant if $\mathbb{F}$ marries. In this case, $\mathbb{F}$'s husbands transfer vertically with probability $\mathring{m}_{\mathrm{V}}$ because the transfer strategy of males may depend on the marriage and paternity strategies of females (males XS and XI, Table A.1a). If this is the case, $\mathring{m}_{\mathrm{V}} \neq m_{\mathrm{V}}$ for a mutant focal female whose marriage and/or paternity strategy differs from the strategy of resident females. $\mathring{m}_{\mathrm{V}} = m_{\mathrm{V}}$ in all other cases.

A.1.4 Coefficients of relatedness

For simplicity, we assume that the biological fathers of the offspring of a promiscuous female are not related, and that the h husbands of a polyandrous female are not related and have equal probability of fathering her offspring. Under these assumptions, and assuming that p in the parent generation is equal to p in the previous generation, a female is related to her offspring by 1/2, a male to his wife's offspring by an

average of $p/2h$, and siblings by an average of $(1 + p^2/h)/4$. Thus, $r_{\mathbb{FF}'} = 1/2$, $r_{\mathbb{FB}'} = (p/2h)[(1 + p^2/h)/4]$, and $r_{\mathbb{MF}'} = (1/2)[(1 + p^2/h)/4]$.

$r_{\mathbb{MB}'}$ must accommodate the fact that the paternity strategy of females may depend on the marriage strategy of males (females XA and XN, Table A.1b). If this is the case, $\mathring{p} \neq p$ for a mutant focal male whose marriage strategy differs from the strategy of resident males. $\mathring{p} = p$ in all other cases. Because a female's h husbands have equal probability of fathering her offspring, the coefficient of relatedness between a focal male $\mathbb{M}$ and his wife's offspring $\mathbb{B}'$ is affected both by the paternity strategy his wife plays against him, and by the paternity strategy she plays against her other $h - 1$ husbands. This can be written as

$$r_{\mathbb{MB}'} = \frac{(1/h)\mathring{p} + [(h-1)/h]p}{2h} = \frac{\mathring{p} + (h-1)p}{2h^2},$$

which reduces to $p/2h$ for $\mathring{p} = p$.

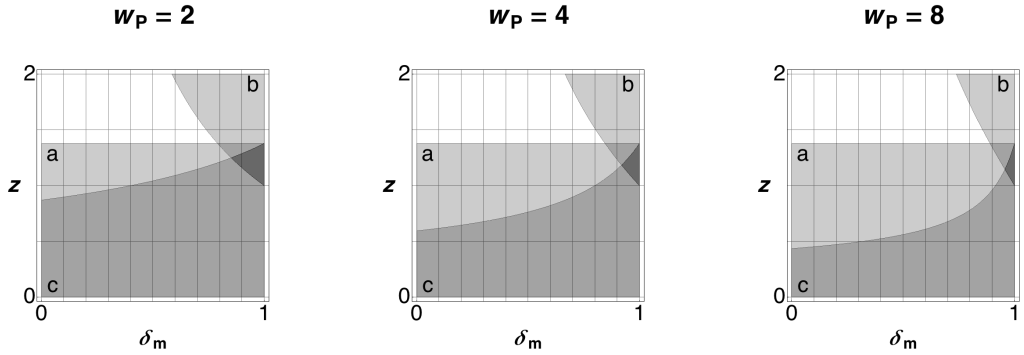
A.2 Stability of social monogamy

The possible combinations of male and female strategies differ in inclusive fitness payoffs; given these payoffs, we can derive evolutionarily stable equilibria consisting of pairs of male and female strategies that cannot be invaded by rare mutants playing alternative strategies (Maynard Smith 1982). The software Mathematica (Wolfram Research, Inc. 2007) was used to perform the numerical analysis and to produce the stability plots.

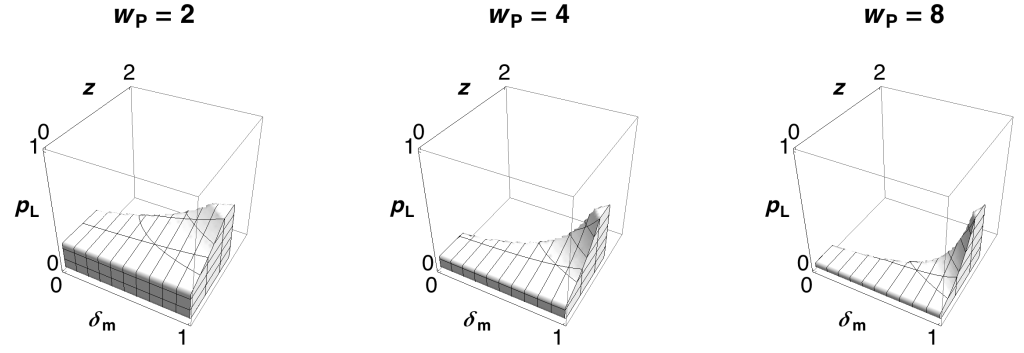
Only two pairs of pure stable strategies result in social monogamy: (MS, MH) and (MS, MA). Because the model does not yield simple analytical solutions, we describe in detail the analytical results for the simplest case, $p_{\mathrm{H}} = 1$; these are plotted in Figure 2.2. Figure A.1 shows graphical results obtained with numerical methods for $p_{\mathrm{H}} = 0.5$.

A.2.1 Stability of (MS, MH)

In the first scenario, (MS, MH), resident males are monogamous and suspicious, that is, they transfer vertically if females are monogamous and provide "high" paternity, diagonally otherwise. Resident females are monogamous and always provide "high" paternity. This combination of male and female strategies results in monogamous marriage, vertical transfer, and "high" paternity (Table A.1).



(a) With monogamous females who always provide "high" paternity



(b) With "astute" monogamous females

Figure A.1: Stability of "suspicious" monogamous males against mutant males with $w_P = 2$, $w_P = 4$, or $w_P = 8$, for $p_H = 0.5$; w_P denotes the number of wives for polygynous males, and p_H the paternity level of males with females who always provide "high" paternity and of monogamous males with "astute" females. δ_m represents the relative male contribution to the resources transferred to the offspring generation; z describes the relationship between resources and individual fitness; p_L represents the paternity level of polygynous males with "astute" females. In (a) social monogamy is stable in the darker area, where all conditions are met; **a** is the condition for stability against monogamous males who transfer diagonally, **b** against polygynous males who transfer vertically, **c** against polygynous males who transfer diagonally. In (b) social monogamy is stable throughout the volume shown.

(MS, MH) is a weak equilibrium, because resident males MS are neutral with males MV, and resident females MH are neutral with females MA. For $p_{\mathrm{H}} = 1$, males MS are stable for

$$z < \frac{\log 3}{\log 2} \quad \text{against males MD and MI,} \tag{A.1a}$$

$$w_{\mathrm{P}}\left(\frac{\delta_{\mathrm{m}}}{w_{\mathrm{P}}} + \delta_{\mathrm{f}}\right)^{z} < 1 \quad \text{against males PV and PS, and} \tag{A.1b}$$

$$(2\delta_{\mathrm{m}} + \delta_{\mathrm{f}} + w_{\mathrm{P}}\delta_{\mathrm{f}})^{z} < 3 \quad \text{against males PD and PI,} \tag{A.1c}$$

where $w_{\mathrm{P}} > 1$ denotes the number of wives for a polygynous male.

These conditions are derived by comparing the inclusive fitness payoff for a resident male to the payoff for mutant males. The payoff for a resident focal male $\mathbb{M}$ is given by the resources $\beta_1 = \delta_{\mathrm{m}} + \delta_{\mathrm{f}} = 1$ he transfers to $\mathbb{B}'$, and by the resources $\phi_4 = \delta_{\mathrm{m}} + \delta_{\mathrm{f}} = 1$ his sister's husband $\mathbb{A}$ transfers to $\mathbb{F}'$ (Figure 2.1). Thus, $\delta_{\mathbb{B}'} = \delta_{\mathrm{m}} + \delta_{\mathrm{f}} = 1$ and $\delta_{\mathbb{F}'} = \delta_{\mathrm{m}} + \delta_{\mathrm{f}} = 1$, with inclusive fitness value for $\mathbb{M}$ $(\delta_{\mathrm{m}} + \delta_{\mathrm{f}})^{z}(1/2)$ and $(\delta_{\mathrm{m}} + \delta_{\mathrm{f}})^{z}(1/4)$, respectively. Because $\delta_{\mathbb{B}'} = 1$ and $\delta_{\mathbb{F}'} = 1$, the inclusive fitness value of these resources is not affected by z (i.e. $\delta^{z}_{\mathbb{B}'} = 1$ and $\delta^{z}_{\mathbb{F}'} = 1$).

The payoff for a mutant focal male $\mathbb{M}$ who is monogamous and transfers diagonally (males MD and MI in this population; Table A.1a) is given by the resources $\phi_2 = \delta_{\mathrm{m}} + \delta_{\mathrm{f}} = 1$ he transfers to $\mathbb{F}'$, and by the resources $\phi_4 = \delta_{\mathrm{m}} + \delta_{\mathrm{f}} = 1$ male $\mathbb{A}$ transfers to $\mathbb{F}'$ (Figure 2.1). Thus, $\delta_{\mathbb{B}'} = 0$, while $\delta_{\mathbb{F}'} = 2\delta_{\mathrm{m}} + 2\delta_{\mathrm{f}} = 2$, with inclusive fitness value for $\mathbb{M}$ $(2\delta_{\mathrm{m}} + 2\delta_{\mathrm{f}})^{z}(1/4)$. Note that $\delta^{z}_{\mathbb{F}'} > 2$ for $z > 1$, that is, values of $z > 1$ result in a greater than twofold increase in fitness for $\mathbb{F}'$. Condition (A.1a) specifies that vertical transfer can be advantageous where the benefit to a mutant male of providing extra resources to his sister's offspring is offset by their lower relatedness relative to wife's offspring (i.e. for $z < \log 3/\log 2$).

The payoff for a mutant focal male $\mathbb{M}$ who is polygynous and transfers vertically (males PV and PS in this population; Table A.1a) is given by the resources $\beta_1 = (\delta_{\mathrm{m}} + w_{\mathrm{P}}\delta_{\mathrm{f}})/w_{\mathrm{P}}$ he transfers to each $\mathbb{B}'$, and by the resources $\phi_4 = \delta_{\mathrm{m}} + \delta_{\mathrm{f}} = 1$ male $\mathbb{A}$ transfers to $\mathbb{F}'$ (Figure 2.1). Thus, $\delta_{\mathbb{B}'} = (\delta_{\mathrm{m}} + w_{\mathrm{P}}\delta_{\mathrm{f}})/w_{\mathrm{P}}$ and $\delta_{\mathbb{F}'} = \delta_{\mathrm{m}} + \delta_{\mathrm{f}} = 1$, with inclusive fitness value for $\mathbb{M}$ $w_{\mathrm{P}}[(\delta_{\mathrm{m}} + w_{\mathrm{P}}\delta_{\mathrm{f}})/w_{\mathrm{P}}]^{z}(1/2)$ and $(\delta_{\mathrm{m}} + \delta_{\mathrm{f}})^{z}(1/4)$, respectively.

Note that $\delta_{\mathbb{B}'} < 1$ if $\mathbb{M}$ contributes at least part of the resources transferred to the next generation (i.e. if $\delta_{\mathrm{m}} > 0$), thus $\delta_{\mathbb{B}'}^{z} < 1$ for $z > 1$, that is, values of $z > 1$ result in a reduction in the fitness value of the resources. Condition (A.1b) specifies that monogamous marriage can be advantageous if the fitness value of resources is depleted through division (i.e. for $\delta_{\mathrm{m}} > 0$ if $z > 1$), and becomes increasingly advantageous as each female provides a relatively smaller share of the resources inherited by her offspring (i.e. as δ_{m} increases and/or w_{P} decreases).

Finally, the payoff for a mutant focal male $\mathbb{M}$ who is polygynous and transfers diagonally (males PD and PI in this population; Table A.1a) is given by the resources $\phi_2 = \delta_{\mathrm{m}} + w_{\mathrm{P}}\delta_{\mathrm{f}} \geq 1$ he transfers to $\mathbb{F}'$, and by the resources $\phi_4 = \delta_{\mathrm{m}} + \delta_{\mathrm{f}} = 1$ male $\mathbb{A}$ transfers to $\mathbb{F}'$ (Figure 2.1). Thus, $\delta_{\mathbb{B}'} = 0$, while $\delta_{\mathbb{F}'} = 2\delta_{\mathrm{m}} + \delta_{\mathrm{f}}(w_{\mathrm{P}} + 1) \geq 2$, with inclusive fitness value for $\mathbb{M}$ $[2\delta_{\mathrm{m}} + \delta_{\mathrm{f}}(w_{\mathrm{P}} + 1)]^{z}(1/4)$. Note that, as for (A.1a), $\delta_{\mathbb{F}'}^{z} > 2$ for $z > 1$, that is, values of $z > 1$ result in a greater than twofold increase in fitness for $\mathbb{F}'$. Condition (A.1c) specifies that vertical transfer can be advantageous where the benefit to a mutant male of providing extra resources to his sister's offspring is offset by their lower relatedness relative to wife's offspring; additionally, it becomes increasingly advantageous as each female provides a relatively smaller share of the resources inherited by her offspring (i.e. as δ_{m} increases and/or w_{P} decreases). Condition (A.1c) reduces to (A.1a) for $\delta_{\mathrm{m}} = 1$.

For $p_{\mathrm{H}} = 1$, the payoff for females MH includes the fitness contribution by their offspring and the fitness contribution by their brother's wife's offspring. Because resident males are suspicious, this is always greater than the payoff for mutant females who are polyandrous and/or provide "low" paternity (females XL, XN, PH, and PA in this population; Table A.1b), which is limited to the fitness contribution by their brother's wife's offspring (and possibly α_{L}).

Thus, (MS, MH) is stable for values of δ_{m} and z for which conditions (A.1a) to (A.1c) are satisfied simultaneously (Figure 2.2a). The upper limit to the range of values of z is given by condition (A.1c), marked **c** in Figure 2.2a, and the lower limit by condition (A.1b), marked **b** in Figure 2.2a; condition (A.1a), marked **a** in Figure 2.2a, is always satisfied where (A.1c) is satisfied.

A.2.2 Stability of (MS, MA)

In the second scenario, (MS, MA), resident males are monogamous and suspicious, that is, they transfer vertically if females are monogamous and provide "high" paternity, diagonally otherwise. Resident females are monogamous and astute, that is, they provide "high" paternity if males are monogamous, "low" paternity otherwise. As for (MS, MH), this combination of male and female strategies results in monogamous marriage, vertical transfer, and "high" paternity (Table A.1).

(MS, MA) is a weak equilibrium, because resident males MS are neutral with males MV, and resident females MA are neutral with females MH. For $p_{\mathrm{H}} = 1$, males MS are stable for

$$z < \frac{\log 3}{\log 2} \quad \text{against males MD and MI,} \tag{A.2a}$$

$$w_{\mathrm{P}}\left(\frac{\delta_{\mathrm{m}}}{w_{\mathrm{P}}} + \delta_{\mathrm{f}}\right)^{z} p_{\mathrm{L}} < 1 \quad \text{against males PV and PI, and} \tag{A.2b}$$

$$(2\delta_{\mathrm{m}} + \delta_{\mathrm{f}} + w_{\mathrm{P}}\delta_{\mathrm{f}})^{z} < 3 \quad \text{against males PD and PS.} \tag{A.2c}$$

As in the previous case, these conditions are derived by comparing the inclusive fitness payoff for a resident male to the payoff for mutant males. The inclusive fitness payoff for a resident focal male $\mathbb{M}$ is identical to the payoff derived for the previous scenario.

Condition (A.2a) is the condition for the stability of resident males MS against invasion by mutant males who are monogamous and transfer diagonally (males MD and MI in this population; Table A.1a), and is identical to (A.1a).

As for (A.1b), the payoff for a mutant focal male $\mathbb{M}$ who is polygynous and transfers vertically (males PV and PI in this population; Table A.1a) is given by the resources $\beta_1 = (\delta_{\mathrm{m}} + w_{\mathrm{P}}\delta_{\mathrm{f}})/w_{\mathrm{P}}$ he transfers to each $\mathbb{B}'$, and by the resources $\phi_4 = \delta_{\mathrm{m}} + \delta_{\mathrm{f}} = 1$ male $\mathbb{A}$ transfers to $\mathbb{F}'$ (Figure 2.1). Thus, $\delta_{\mathbb{B}'} = (\delta_{\mathrm{m}} + w_{\mathrm{P}}\delta_{\mathrm{f}})/w_{\mathrm{P}}$ and $\delta_{\mathbb{F}'} = \delta_{\mathrm{m}} + \delta_{\mathrm{f}} = 1$; because in this case resident females give polygynous males paternity p_{L}, these resources have inclusive fitness value for $\mathbb{M}$ $w_{\mathrm{P}}[(\delta_{\mathrm{m}} + w_{\mathrm{P}}\delta_{\mathrm{f}})/w_{\mathrm{P}}]^{z}(p_{\mathrm{L}}/2)$ and $(\delta_{\mathrm{m}} + \delta_{\mathrm{f}})^{z}(1/4)$, respectively. As for (A.1b), $\delta_{\mathbb{B}'} < 1$ if $\mathbb{M}$ contributes at least part of the resources

transferred to the next generation (i.e. if $\delta_{\mathrm{m}} > 0$), thus $\delta_{\mathbb{B}'}^{z} < 1$ for $z > 1$, that is, values of $z > 1$ result in a reduction in the fitness value of the resources. However, because of the reduction in relatedness between polygynous males and their wives' offspring, condition (A.2b) specifies that monogamy can be advantageous irrespective of whether the fitness value of resources is depleted through division (i.e. for $z > 0$). As for (A.1b), monogamy becomes increasingly advantageous as each female provides a relatively smaller share of the resources inherited by her offspring (i.e. as δ_{m} increases and/or w_{P} decreases). Additionally, monogamy becomes increasingly advantageous as the relatedness between a polygynous male and his wives' offspring decreases (i.e. as p_{L} decreases); for $p_{\mathrm{L}} < 1/w_{\mathrm{P}}$, any potential fitness benefit to polygyny is offset by the reduction in relatedness to wives' offspring, such that monogamy is stable for all values of δ_{m}.

Finally, condition (A.2c) is the condition for stability against mutant males who are polygynous and transfer diagonally (males PD and PS in this population, Table A.1a), and is identical to (A.1c).

For $p_{\mathrm{H}} = 1$, the payoff for females MA is always greater than the payoff for mutant females who are polyandrous and/or provide "low" paternity (females XL, XN, PH, and PA in this population; Table A.1b): as in the previous scenario, the former includes the fitness contribution by own offspring and brother's wife's offspring, while the latter is limited to the fitness contribution by brother's wife's offspring (and possibly α_{L}).

Thus, (MS, MA) is stable for values of δ_{m}, z, and p_{L} for which conditions (A.2a) to (A.2c) are satisfied simultaneously (Figure 2.2b). The upper limit to the range of values of z is given by condition (A.2c) and the lower limit by condition (A.2b); condition (A.2a) is always satisfied where (A.2c) is satisfied.

Appendix B

Cross-cultural data

In this appendix I present the cross-cultural data used for the log-linear analysis in Chapter 3 (Section B.1) and for the phylogenetic comparative analyses in Chapters 4 to 6 (Section B.2); maps of their geographical distribution are, respectively, in Figures B.1 and B.2. The maps are shown on the same scale to illustrate the difference in scale of analysis afforded by the two approaches.

B.1 *SCCS* data

Table B.1 includes the recoded data in binary form on marriage strategy, transfer strategies for land and for movables, and religious affiliation, for the 186 societies in the *SCCS* (Section 3.2.1). Only the 87 societies with data on all variables were included in the log-linear analysis; the corresponding entries are italicized in Table B.1 and represented by dots in Figures B.1b to B.1e.

Information on language family is included in Table B.1 to illustrate the distribution of *SCCS* societies across linguistic phyla.

Table B.1: Recoded *SCCS* data

SCCS identifiers[1]		Marriage[2]	Land[3]	Movables[4]	Religion[5]	Language family[6]
Code	Name					
1	*Nama Hottentot*	*Polygynous*	*Other*	*Vertical*	*Other*	*Khoisan*
2	Kung Bushmen	Polygynous	Other	Other	–	Khoisan
3	Thonga	Polygynous	Other	Vertical	–	Niger-Congo
4	Lozi	Polygynous	Vertical	Vertical	–	Niger-Congo
5	Mbundu	Polygynous	Vertical	Other	–	Niger-Congo
6	Suku	Polygynous	Other	Other	–	Niger-Congo
7	*Bemba*	*Polygynous*	*Other*	*Other*	*Other*	*Niger-Congo*
8	Nyakyusa	Polygynous	Vertical	Vertical	–	Niger-Congo
9	*Hadza*	*Polygynous*	*Other*	*Vertical*	*Other*	*Khoisan*
10	Luguru	Polygynous	Other	Vertical	–	Niger-Congo
11	*Kikuyu*	*Polygynous*	*Vertical*	*Vertical*	*Other*	*Niger-Congo*
12	Ganda	Polygynous	Vertical	Vertical	–	Niger-Congo
13	*Mbuti Pygmies*	*Polygynous*	*Other*	*Vertical*	*Other*	*Niger-Congo*
14	Nkundo Mongo	Polygynous	Vertical	Vertical	–	Niger-Congo
15	Banen	Polygynous	Vertical	Vertical	–	Niger-Congo
16	Tiv	Polygynous	Other	Vertical	–	Niger-Congo
17	Ibo	Polygynous	Vertical	Vertical	–	Niger-Congo
18	Fon	Polygynous	Vertical	Vertical	–	Niger-Congo
19	*Ashanti*	*Polygynous*	*Other*	*Other*	*Other*	*Niger-Congo*
20	*Mende*	*Polygynous*	*Vertical*	*Vertical*	*Other*	*Niger-Congo*
21	*Wolof*	*Polygynous*	*Vertical*	*Vertical*	*Other*	*Niger-Congo*
22	*Bambara*	*Polygynous*	*Vertical*	*Vertical*	*Other*	*Niger-Congo*
23	*Tallensi*	*Polygynous*	*Vertical*	*Vertical*	*Other*	*Niger-Congo*
24	*Songhai*	*Polygynous*	*Vertical*	*Vertical*	*Other*	*Nilo-Saharan*

Continued on next page

Table B.1: Recoded *SCCS* data (continued from previous page)

SCCS identifiers[1]		Marriage[2]	Land[3]	Movables[4]	Religion[5]	Language family[6]
Code	Name					
25	*Fulani*	*Polygynous*	*Other*	*Vertical*	*Other*	*Niger-Congo*
26	*Hausa*	*Polygynous*	*Vertical*	*Vertical*	*Other*	*Afro-Asiatic*
27	Massa	Polygynous	Vertical	Vertical	–	Afro-Asiatic
28	Azande	Polygynous	Vertical	Vertical	–	Niger-Congo
29	*Fur*	*Polygynous*	*Vertical*	*Vertical*	*Other*	*Nilo-Saharan*
30	*Otoro Nuba*	*Polygynous*	*Vertical*	*Vertical*	*Other*	*Niger-Congo*
31	*Shilluk*	*Polygynous*	*Vertical*	*Vertical*	*Other*	*Nilo-Saharan*
32	Mao	Polygynous	Vertical	Vertical	–	Nilo-Saharan
33	*Kafa*	*Polygynous*	*Vertical*	*Vertical*	*Other*	*Afro-Asiatic*
34	Masai	Polygynous	Vertical	Vertical	–	Nilo-Saharan
35	Konso	Polygynous	Vertical	Vertical	–	Afro-Asiatic
36	*Somali*	*Polygynous*	*Vertical*	*Vertical*	*Other*	*Afro-Asiatic*
37	*Amhara*	*Monogamous*	*Vertical*	*Vertical*	*Christianized*	*Afro-Asiatic*
38	*Bogo*	*Polygynous*	*Vertical*	*Vertical*	*Christianized*	*Afro-Asiatic*
39	*Nubians*	*Polygynous*	*Vertical*	*Vertical*	*Other*	*Nilo-Saharan*
40	*Teda*	*Polygynous*	*Vertical*	*Vertical*	*Other*	*Nilo-Saharan*
41	*Tuareg*	*Monogamous*	*Other*	*Vertical*	*Other*	*Afro-Asiatic*
42	*Riffians*	*Polygynous*	*Vertical*	*Vertical*	*Other*	*Afro-Asiatic*
43	*Egyptians*	*Polygynous*	*Vertical*	*Vertical*	*Other*	*Afro-Asiatic*
44	Hebrews	Polygynous	Vertical	Vertical	–	Afro-Asiatic
45	*Babylonians*	*Polygynous*	*Vertical*	*Vertical*	*Other*	*Afro-Asiatic*
46	*Rwala Bedouin*	*Polygynous*	*Other*	*Vertical*	*Other*	*Afro-Asiatic*
47	*Turks*	*Polygynous*	*Vertical*	*Vertical*	*Other*	*Altaic*
48	*Gheg Albanians*	*Polygynous*	*Vertical*	*Vertical*	*Other*	*Indo-European*

Continued on next page

Table B.1: Recoded *SCCS* data (continued from previous page)

SCCS identifiers[1]		Marriage[2]	Land[3]	Movables[4]	Religion[5]	Language family[6]
Code	Name					
49	Romans	Monogamous	Vertical	Vertical	–	Indo-European
50	*Basques*	*Monogamous*	*Vertical*	*Vertical*	*Christianized*	*Isolate*
51	*Irish*	*Monogamous*	*Vertical*	*Vertical*	*Christianized*	*Indo-European*
52	*Lapps*	*Monogamous*	*Vertical*	*Vertical*	*Christianized*	*Uralic-Yukaghir*
53	Yurak Samoyed	Polygynous	–	–	Christianized	Uralic-Yukaghir
54	Russians	Monogamous	Other	–	Christianized	Indo-European
55	Abkhaz	Polygynous	Vertical	Vertical	–	Caucasian
56	*Armenians*	*Monogamous*	*Vertical*	*Vertical*	*Christianized*	*Indo-European*
57	Kurd	Polygynous	Vertical	–	Other	Indo-European
58	*Basseri*	*Polygynous*	*Other*	*Vertical*	*Other*	*Indo-European*
59	*Punjabi*	*Monogamous*	*Vertical*	*Vertical*	*Other*	*Indo-European*
60	*Gond*	*Polygynous*	*Other*	*Other*	*Other*	*Dravidian*
61	Toda	–	Other	Vertical	Other	Dravidian
62	*Santal*	*Polygynous*	*Vertical*	*Vertical*	*Other*	*Austroasiatic*
63	*Uttar Pradesh*	*Polygynous*	*Vertical*	*Vertical*	*Other*	*Indo-European*
64	Burusho	Polygynous	–	–	Other	Isolate
65	*Kazak*	*Polygynous*	*Other*	*Vertical*	*Other*	*Altaic*
66	*Khalka Mongols*	*Monogamous*	*Vertical*	*Vertical*	*Other*	*Altaic*
67	*Lolo*	*Polygynous*	*Vertical*	*Vertical*	*Other*	*Sino-Tibetan*
68	*Lepcha*	*Polygynous*	*Vertical*	*Vertical*	*Other*	*Sino-Tibetan*
69	Garo	Polygynous	Other	Other	–	Sino-Tibetan
70	Lakher	Monogamous	Vertical	Vertical	–	Sino-Tibetan
71	*Burmese*	*Monogamous*	*Vertical*	*Vertical*	*Other*	*Sino-Tibetan*
72	Lamet	Polygynous	Other	Vertical	–	Austroasiatic

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Table B.1: Recoded *SCCS* data (continued from previous page)

SCCS identifiers[1]		Marriage[2]	Land[3]	Movables[4]	Religion[5]	Language family[6]
Code	Name					
73	*Vietnamese*	*Polygynous*	*Vertical*	*Vertical*	*Other*	*Austroasiatic*
74	Rhade	Monogamous	–	–	–	Austronesian
75	Khmer	Polygynous	–	–	Other	Austroasiatic
76	*Siamese*	*Polygynous*	*Vertical*	*Vertical*	*Other*	*Daic*
77	*Semang*	*Polygynous*	*Other*	*Vertical*	*Other*	*Austroasiatic*
78	Nicobarese	Polygynous	Other	Vertical	–	Austroasiatic
79	Andamanese	Monogamous	Other	–	Other	Andaman
80	Vedda	Monogamous	Vertical	Vertical	–	Indo-European
81	*Tanala*	*Polygynous*	*Vertical*	*Vertical*	*Other*	*Austronesian*
82	*Negri Sembilan*	*Polygynous*	*Other*	*Other*	*Other*	*Austronesian*
83	*Javanese*	*Polygynous*	*Vertical*	*Vertical*	*Other*	*Austronesian*
84	*Balinese*	*Monogamous*	*Vertical*	*Vertical*	*Other*	*Austronesian*
85	*Iban*	*Monogamous*	*Vertical*	*Vertical*	*Other*	*Austronesian*
86	Badjau	Polygynous	–	–	–	Austronesian
87	*Toradja*	*Polygynous*	*Vertical*	*Vertical*	*Other*	*Austronesian*
88	*Tobelorese*	*Monogamous*	*Vertical*	*Vertical*	*Christianized*	*West Papuan*
89	Alorese	Polygynous	–	–	–	Trans New Guinea
90	Tiwi	Polygynous	Other	–	–	Australian
91	*Aranda*	*Polygynous*	*Other*	*Vertical*	*Other*	*Australian*
92	Orokaiva	Polygynous	–	–	–	Trans New Guinea
93	Kimam	Polygynous	Vertical	Other	–	Trans New Guinea
94	Kapauku	Polygynous	–	–	–	Trans New Guinea
95	*Kwoma*	*Polygynous*	*Vertical*	*Vertical*	*Other*	*Sepik-Ramu*
96	*Manus*	*Polygynous*	*Other*	*Other*	*Christianized*	*Austronesian*

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Table B.1: Recoded *SCCS* data (continued from previous page)

SCCS identifiers[1]		Marriage[2]	Land[3]	Movables[4]	Religion[5]	Language family[6]
Code	Name					
97	New Ireland	Polygynous	–	Other	Other	Austronesian
98	Trobrianders	Polygynous	Other	Other	–	Austronesian
99	*Siuai*	*Polygynous*	*Other*	*Vertical*	*Christianized*	*East Papuan*
100	Tikopia	Polygynous	Vertical	–	Christianized	Austronesian
101	*Pentecost*	*Polygynous*	*Other*	*Vertical*	*Christianized*	*Austronesian*
102	Mbau Fijians	Polygynous	–	Vertical	–	Austronesian
103	Ajie	Polygynous	–	–	–	Austronesian
104	Maori	Polygynous	Vertical	Vertical	–	Austronesian
105	Marquesans	–	Vertical	Vertical	Other	Austronesian
106	Samoans	Polygynous	–	–	–	Austronesian
107	*Gilbertese*	*Polygynous*	*Vertical*	*Vertical*	*Christianized*	*Austronesian*
108	*Marshallese*	*Polygynous*	*Other*	*Other*	*Christianized*	*Austronesian*
109	*Trukese*	*Polygynous*	*Vertical*	*Vertical*	*Christianized*	*Austronesian*
110	*Yapese*	*Polygynous*	*Other*	*Other*	*Christianized*	*Austronesian*
111	*Palauans*	*Polygynous*	*Other*	*Vertical*	*Christianized*	*Austronesian*
112	Ifugao	Polygynous	Vertical	Vertical	–	Austronesian
113	*Atayal*	*Monogamous*	*Vertical*	*Vertical*	*Other*	*Austronesian*
114	*Chinese*	*Monogamous*	*Vertical*	*Vertical*	*Other*	*Sino-Tibetan*
115	*Manchu*	*Monogamous*	*Vertical*	*Vertical*	*Other*	*Altaic*
116	*Koreans*	*Monogamous*	*Vertical*	*Vertical*	*Other*	*Isolate*
117	*Japanese*	*Monogamous*	*Vertical*	*Vertical*	*Other*	*Isolate*
118	Ainu	Polygynous	–	Vertical	–	Isolate
119	*Gilyak*	*Polygynous*	*Other*	*Vertical*	*Other*	*Isolate*
120	Yukaghir	Monogamous	Other	Vertical	–	Uralic-Yukaghir

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Table B.1: Recoded *SCCS* data (continued from previous page)

SCCS identifiers[1]		Marriage[2]	Land[3]	Movables[4]	Religion[5]	Language family[6]
Code	Name					
121	Chukchee	Polygynous	Other	Vertical	–	Chukchi-Kamchatkan
122	Ingalik	Polygynous	Other	Vertical	–	Na-Dene
123	Aleut	Polygynous	Other	Vertical	–	Eskimo-Aleut
124	Copper Eskimo	Polygynous	Other	Vertical	–	Eskimo-Aleut
125	Montagnais	Polygynous	Vertical	Vertical	–	Algic
126	Micmac	Polygynous	–	–	–	Algic
127	Saulteaux	Polygynous	–	–	Christianized	Algic
128	*Slave*	*Monogamous*	*Other*	*Other*	*Christianized*	*Na-Dene*
129	Kaska	Polygynous	–	Vertical	–	Na-Dene
130	Eyak	Polygynous	–	Other	–	Na-Dene
131	Haida	Polygynous	Other	Other	–	Na-Dene
132	Bellacoola	Polygynous	Other	Vertical	–	Salish
133	*Twana*	*Polygynous*	*Other*	*Other*	*Other*	*Salish*
134	Yurok	Polygynous	–	Vertical	–	Algic
135	*Pomo*	*Polygynous*	*Other*	*Vertical*	*Other*	*Hokan*
136	Yokuts	Polygynous	Other	–	–	California and plateau Penutian
137	*Paiute*	*Polygynous*	*Other*	*Other*	*Other*	*Uto-Aztecan*
138	Klamath	Polygynous	Other	Other	–	California and plateau Penutian
139	*Kutenai*	*Polygynous*	*Other*	*Vertical*	*Other*	*Isolate*
140	Gros Ventre	Polygynous	Other	Other	–	Algic
141	Hidatsa	Polygynous	–	Vertical	Other	Siouan
142	Pawnee	Polygynous	Other	Other	–	Caddoan
143	Omaha	Polygynous	Vertical	Vertical	–	Siouan
144	Huron	Monogamous	–	–	–	Iroquian

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Table B.1: Recoded *SCCS* data (continued from previous page)

SCCS identifiers[1]		Marriage[2]	Land[3]	Movables[4]	Religion[5]	Language family[6]
Code	Name					
145	Creek	Polygynous	–	Vertical	Other	Natchez-Muskogean
146	Natchez	Polygynous	–	–	–	Natchez-Muskogean
147	*Comanche*	*Polygynous*	*Other*	*Other*	*Other*	*Uto-Aztecan*
148	Chiricahua	Polygynous	Other	Other	–	Na-Dene
149	Zuni	Monogamous	Other	Vertical	–	Isolate
150	Havasupai	Polygynous	Vertical	Other	–	Hokan
151	*Papago*	*Polygynous*	*Vertical*	*Other*	*Other*	*Uto-Aztecan*
152	*Huichol*	*Polygynous*	*Vertical*	*Vertical*	*Christianized*	*Uto-Aztecan*
153	*Aztec*	*Polygynous*	*Vertical*	*Vertical*	*Other*	*Uto-Aztecan*
154	*Popoluca*	*Polygynous*	*Vertical*	*Vertical*	*Christianized*	*Macro-Mayan*
155	*Quiche*	*Monogamous*	*Vertical*	*Vertical*	*Christianized*	*Macro-Mayan*
156	Miskito	Polygynous	–	–	Christianized	Chibcha-Misumalpan
157	Bribri	Polygynous	Other	Vertical	–	Chibcha-Misumalpan
158	Cuna	Polygynous	–	–	–	Chibcha-Misumalpan
159	Goajiro	Polygynous	–	Other	–	Macro-Arawakan
160	*Haitians*	*Polygynous*	*Vertical*	*Vertical*	*Christianized*	*Indo-European*
161	Callinago	Polygynous	–	–	Other	Macro-Arawakan
162	Warrau	Polygynous	Other	–	–	Macro-Paezan
163	Yanomamo	Polygynous	Other	–	Other	Macro-Panoan
164	Carib	Polygynous	–	–	–	Tupi-Carib
165	Saramacca	Polygynous	–	Other	Other	Indo-European
166	Mundurucu	Polygynous	Other	Other	–	Tupi-Carib
167	*Cubeo*	*Polygynous*	*Other*	*Vertical*	*Other*	*Tucanoan*
168	Cayapa	Monogamous	–	–	–	Macro-Paezan

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Table B.1: Recoded *SCCS* data (continued from previous page)

SCCS identifiers[1]		Marriage[2]	Land[3]	Movables[4]	Religion[5]	Language family[6]
Code	Name					
169	*Jivaro*	*Polygynous*	*Other*	*Vertical*	*Other*	*Jivaroan*
170	Amahuaca	Polygynous	Other	Other	–	Macro-Panoan
171	*Inca*	*Polygynous*	*Other*	*Vertical*	*Other*	*Quechumaran*
172	*Aymara*	*Monogamous*	*Vertical*	*Vertical*	*Christianized*	*Quechumaran*
173	*Siriono*	*Polygynous*	*Other*	*Other*	*Other*	*Tupi-Carib*
174	Nambicuara	Polygynous	Other	Other	–	Nambiquaran
175	Trumai	Polygynous	Other	–	Other	Macro-Arawakan
176	Timbira	Monogamous	Other	Vertical	–	Macro Ge
177	Tupinamba	Polygynous	–	–	Other	Tupi-Carib
178	Botocudo	Polygynous	Other	–	–	Macro Ge
179	*Shavante*	*Polygynous*	*Other*	*Other*	*Other*	*Macro Ge*
180	Aweikoma	Polygynous	Other	Other	–	Macro Ge
181	Cayua	Polygynous	–	–	Other	Tupi-Carib
182	Lengua	Polygynous	Other	–	–	Mascoian
183	Abipon	Polygynous	Other	–	–	Guaykuruan
184	Mapuche	Polygynous	Vertical	Vertical	–	Araucanian
185	Tehuelche	Polygynous	Other	–	Other	Araucanian
186	Yahgan	Polygynous	Other	Other	–	Isolate

[1] After Murdock and White (1969). Only the 87 entries in italics were included in the log-linear analysis (Section 3.3).

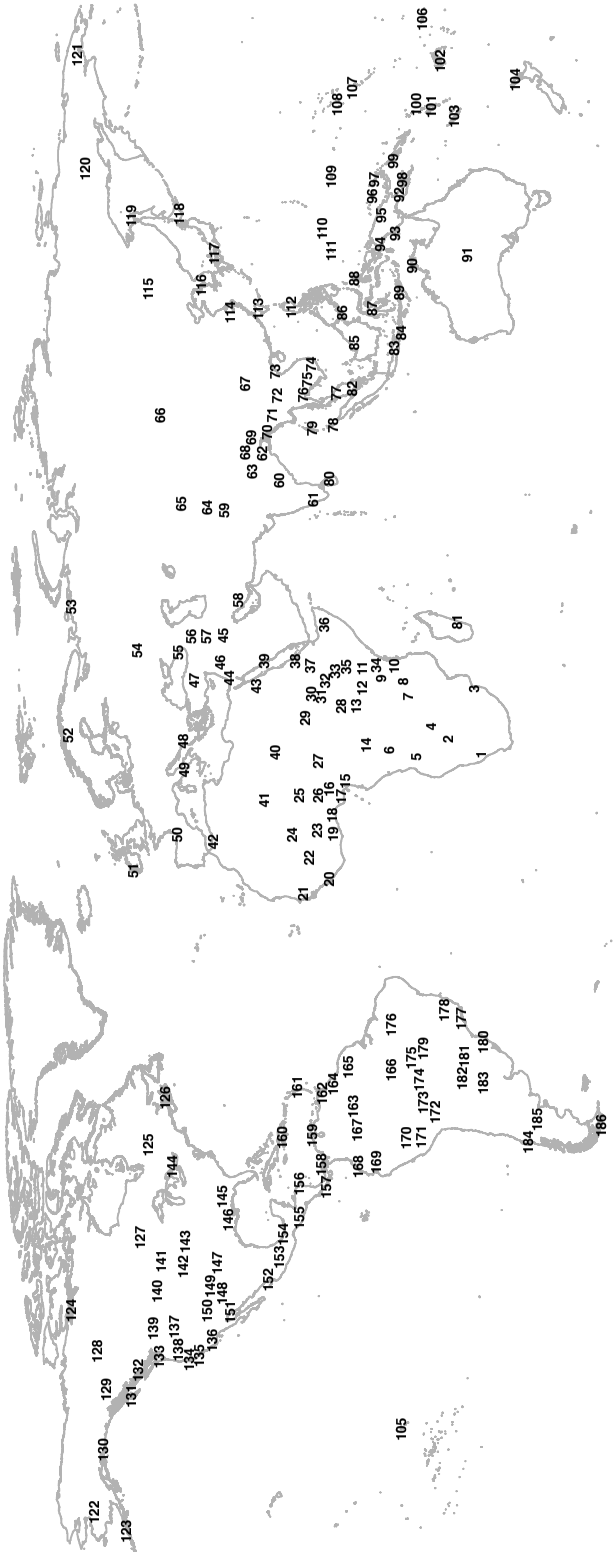
[2] Marriage strategy. Recoded from *SCCS* variable 79 (Section 3.2.1.1).

[3] Transfer strategy for land. Recoded from *SCCS* variable 278 (Section 3.2.1.2).

[4] Transfer strategy for movables. Recoded from *SCCS* variable 279 (Section 3.2.1.2).

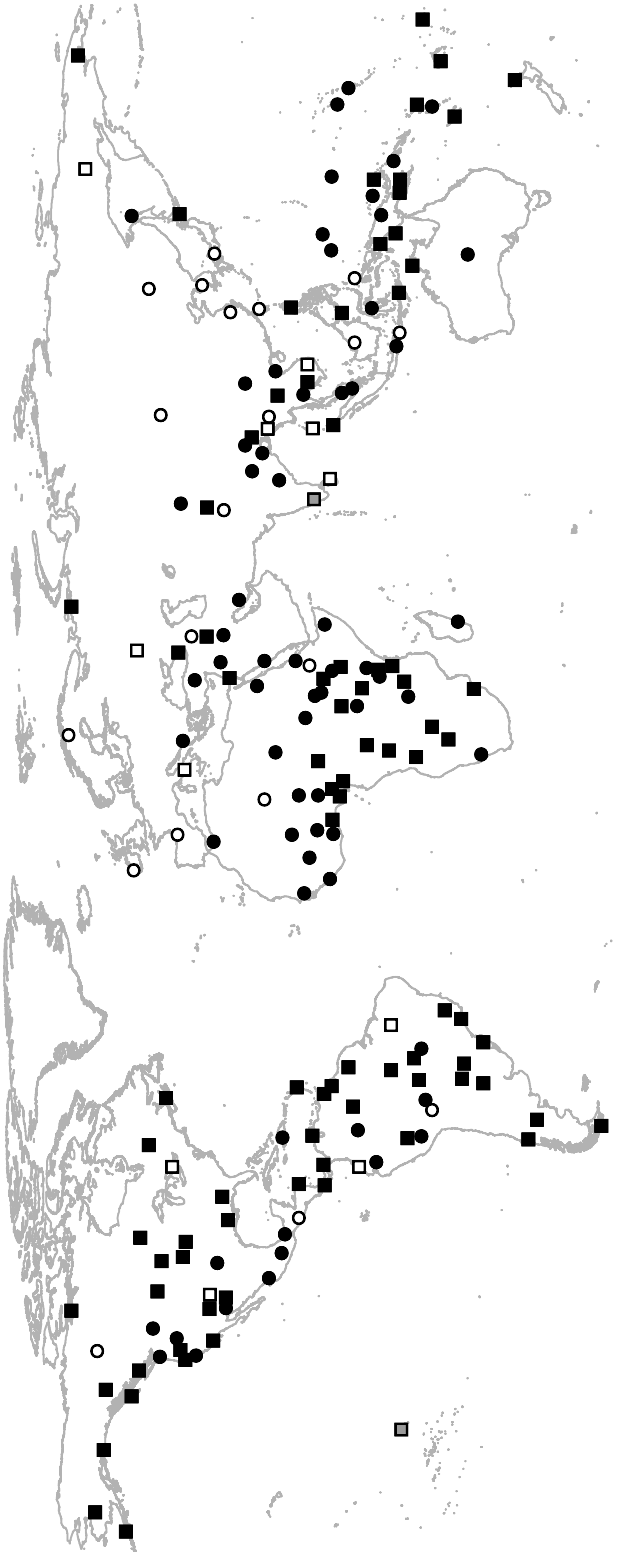
[5] Religious affiliation. Recoded from *SCCS* variables 713 and 2002 (Section 3.2.1.3).

[6] After Burton (1999).



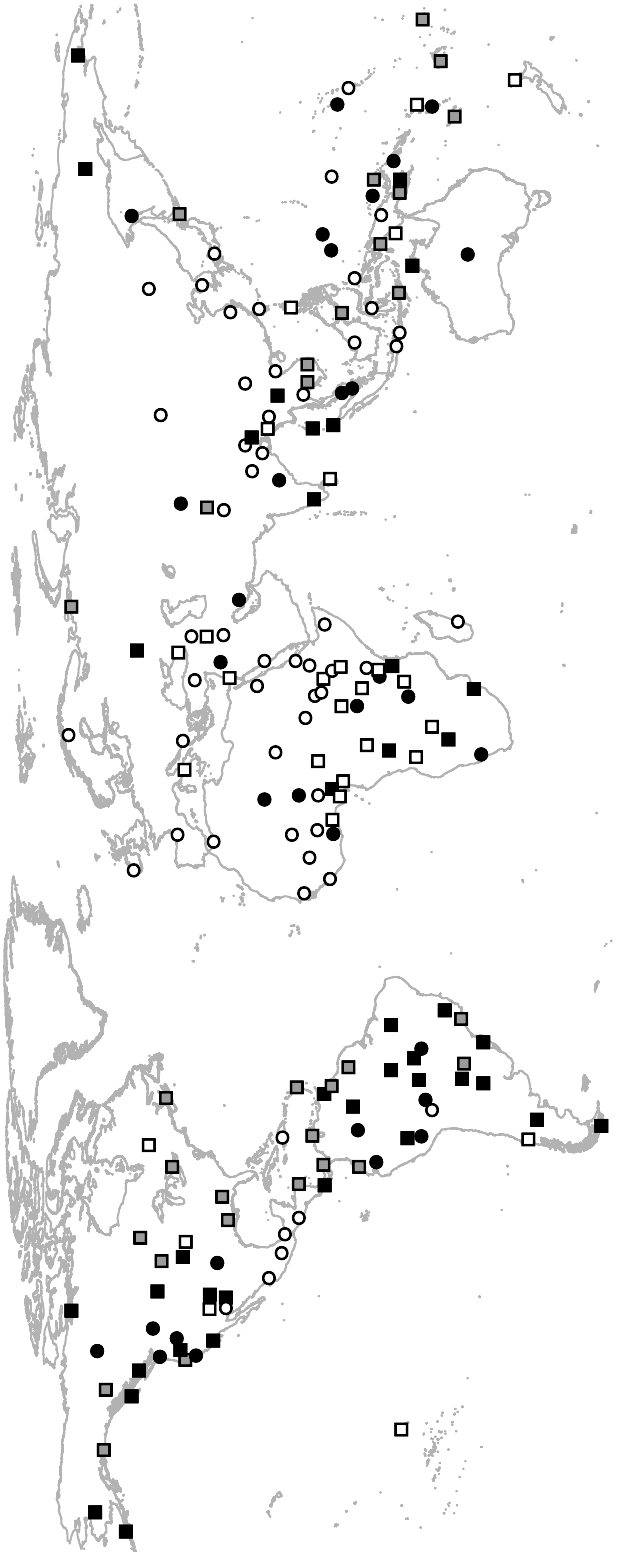
(a) *SCCS* code

Figure B.1: Map illustrating the geographic distribution of the recoded *SCCS* data in Table B.1. Entries included in the log-linear analysis are italicized in Table B.1.



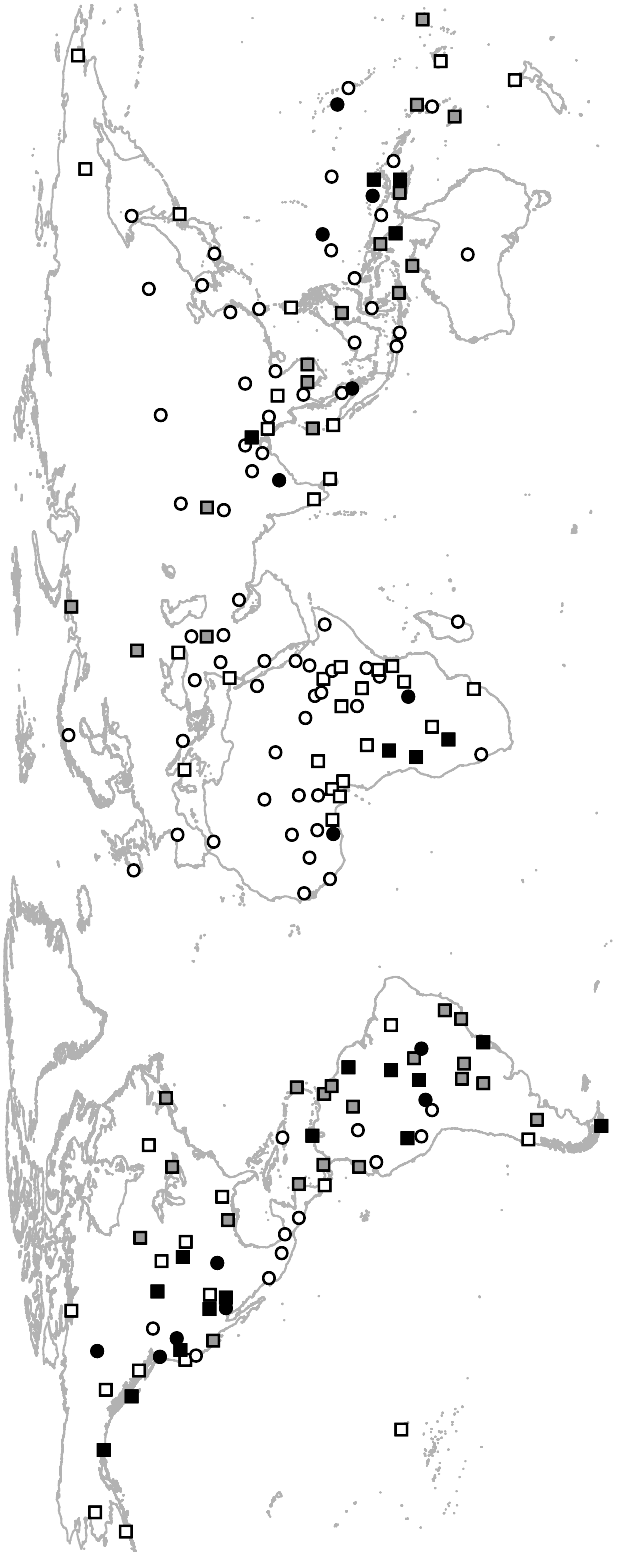
(b) Marriage strategy

Figure B.1: Map illustrating the geographic distribution of the recoded *SCCS* data in Table B.1. Entries included in the log-linear analysis are marked by dots; colours express the marriage strategy (white: monogamous; black: polygynous; grey: missing).



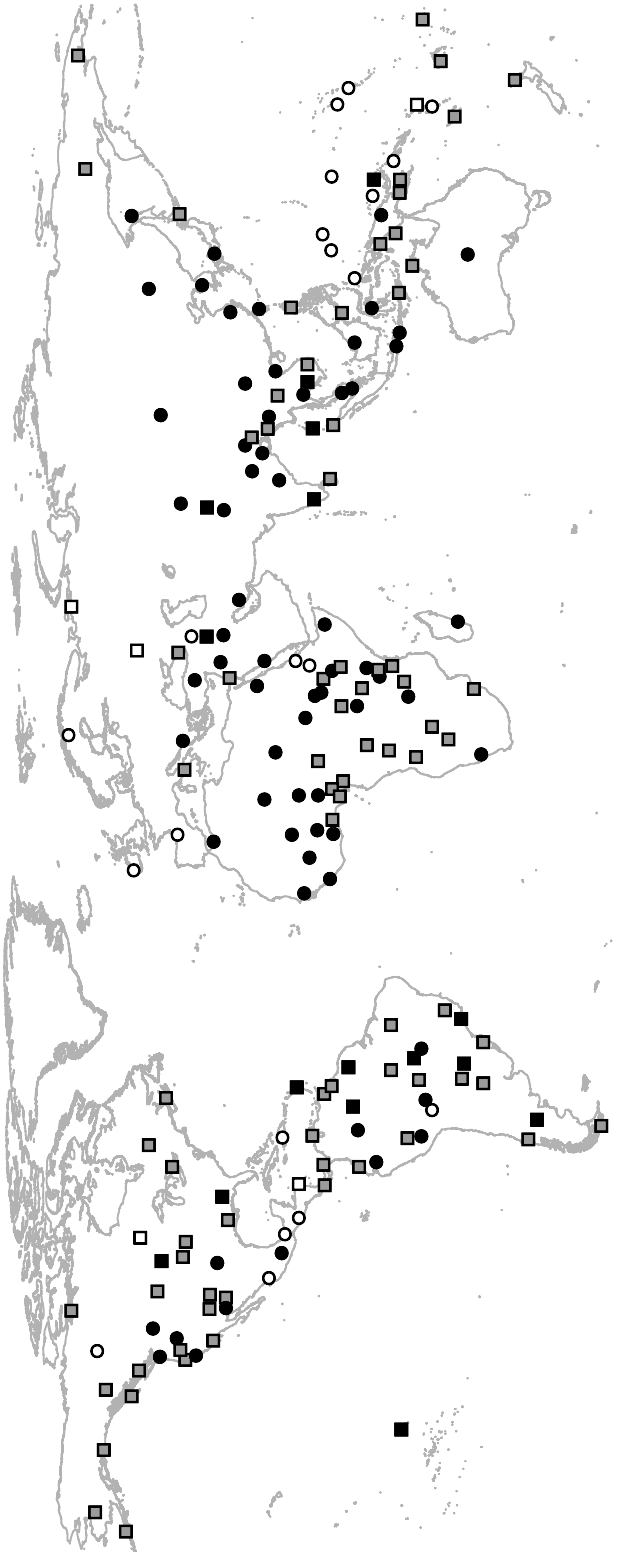
(c) Transfer strategy for land

Figure B.1: Map illustrating the geographic distribution of the recoded *SCCS* data in Table B.1. Entries included in the log-linear analysis are marked by dots; colours express the transfer strategy for land (white: vertical; black: other; grey: missing).



(d) Transfer strategy for movables

Figure B.1: Map illustrating the geographic distribution of the recoded *SCCS* data in Table B.1. Entries included in the log-linear analysis are marked by dots; colours express the transfer strategy for movables (white: vertical; black: other; grey: missing).



(e) Religious affiliation

Figure B.1: Map illustrating the geographic distribution of the recoded *SCCS* data in Table B.1. Entries included in the log-linear analysis are marked by dots; colours express the religious affiliation (white: Christianized; black: other; grey: missing).

B.2 *EA* data

Table B.2 includes the recoded data on marriage strategy and residence strategy (prevailing and alternative modes) for the 27 societies in the *EA* that could be matched to speech varieties in Dyen et al.'s (1992) linguistic database (Section 4.2.1).

The prevailing and alternative modes of residence are shown, respectively, in Figure B.2c and Figure B.2d; Figure B.2e shows the same data in binary form, combined as neolocal/non-neolocal and over the two modes of residence (Section 6.2.1).

As indicated in the captions to Figures B.2b to B.2e, the colour schemes match those used in the relevant figures in Chapters 4 to 6.

Table B.2: Recoded *EA* data

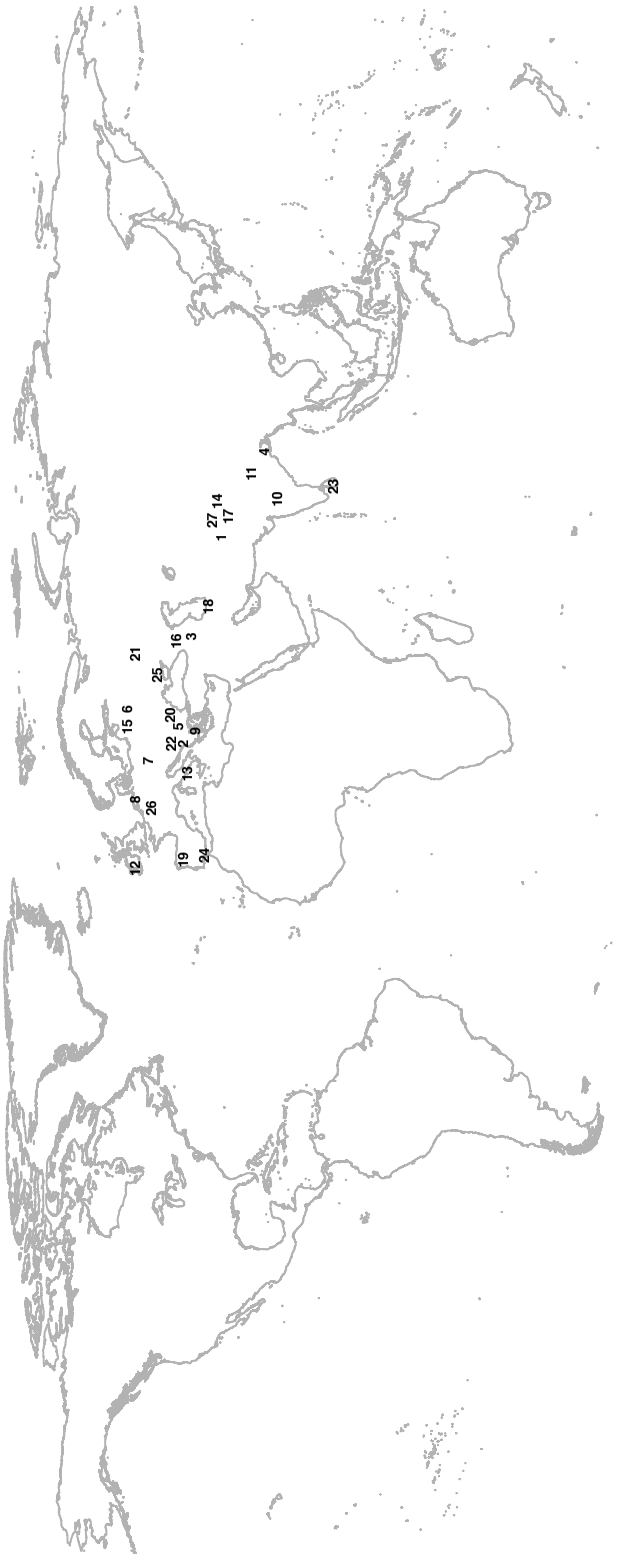
Key[1]	Speech variety[2]	*EA* identifiers[3]		Marriage strategy[4]	Residence strategy[5]	
		Code	Name		Prevailing mode	Alternative mode
1	Afghan	Ea11	Afghans	Polygynous	Virilocal	Virilocal
2	Albanian G	Ce1	Gheg	Polygynous	Virilocal	Virilocal
3	Armenian Mod	Ci10	Armenians	Monogamous	Virilocal	Uxorilocal
4	Bengali	Ef2	Bengali	Polygynous	Virilocal	Virilocal
5	Bulgarian	Ch5	Bulgarians	Monogamous	Virilocal	Neolocal
6	Byelorussian	Ch6	Byelorussians	Monogamous	Ambilocal	Neolocal
7	Czech	Ch3	Czechs	Monogamous	Virilocal	Neolocal
8	Dutch List	Cg1	Dutch	Monogamous	Ambilocal	Neolocal
9	Greek MD	Ce7	Greeks	Monogamous	Virilocal	Neolocal
10	Gujarati	Ef9	Gujarati	Polygynous	Virilocal	Virilocal
11	Hindi	Ef11	Uttar Pradesh	Polygynous	Virilocal	Virilocal
12	Irish B	Cg3	Irish	Monogamous	Virilocal	Neolocal
13	Italian	Ce5	Neapolitans	Monogamous	Neolocal	Uxorilocal
14	Kashmiri	Ef8	Kashmiri	Polygynous	Virilocal	Virilocal
15	Lithuanian ST	Ch9	Lithuanians	Monogamous	Virilocal	Neolocal
16	Ossetic	Ci6	Osset	Polygynous	Virilocal	Virilocal
17	Panjabi ST	Ea13	Punjabi	Monogamous	Virilocal	Virilocal
18	Persian List	Ea9	Iranians	Polygynous	Virilocal	Neolocal
19	Portuguese ST	Ce2	Portuguese	Monogamous	Virilocal	Neolocal
20	Rumanian List	Ch10	Romanians	Monogamous	Neolocal	Virilocal
21	Russian	Ch11	Russians	Monogamous	Neolocal	Neolocal
22	Serbocroatian	Ch1	Serbs	Monogamous	Virilocal	Neolocal
23	Singhalese	Eh6	Sinhalese	Monogamous	Virilocal	Uxorilocal
24	Spanish	Ce6	Spaniards	Monogamous	Neolocal	Neolocal

Continued on next page

Table B.2: Recoded *EA* data (continued from previous page)

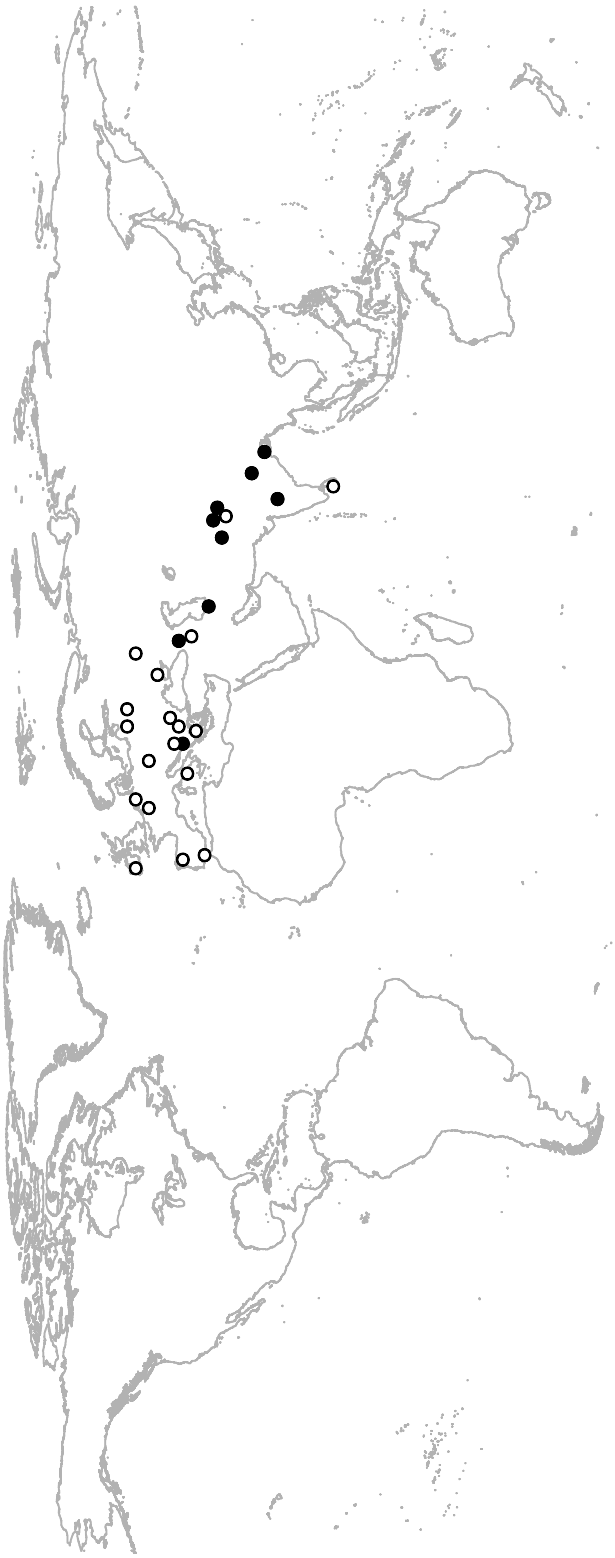
Key[1]	Speech variety[2]	*EA* identifiers[3]		Marriage strategy[4]	Residence strategy[5]	
		Code	Name		Prevailing mode	Alternative mode
25	Ukrainian	Ch7	Ukrainians	Monogamous	Virilocal	Neolocal
26	Walloon	Cg5	Walloons	Monogamous	Neolocal	Neolocal
27	Waziri	Ea2	Pathan	Polygynous	Virilocal	Virilocal

[1] Refers to the numbers in Figure B.2a.
[2] After Dyen et al. (1992) (Section 4.2.1).
[3] After Gray (1999) (Section 4.2.1).
[4] Recoded from *EA* variable 9 (Section 4.2.1).
[5] Recoded from *EA* variable 12 for prevailing mode and 14 for alternative mode (Section 5.2.1).



(a) Key

Figure B.2: Map illustrating the geographic distribution of the recoded *EA* data in Table B.2. Numbers correspond to entries in the relevant column in Table B.2.

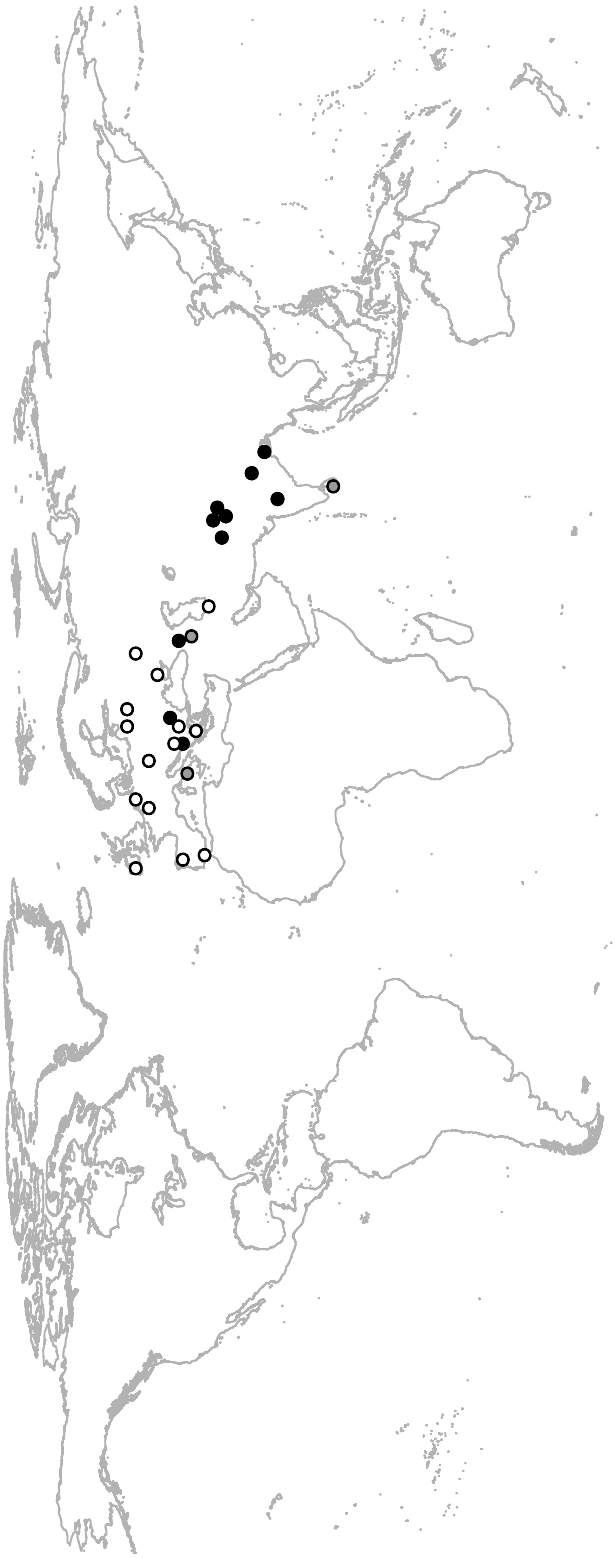


(b) Marriage strategy

Figure B.2: Map illustrating the geographic distribution of the recoded *EA* data in Table B.2. Colours express the marriage strategy (white: monogamous; black: polygynous), as per Figure 4.4.

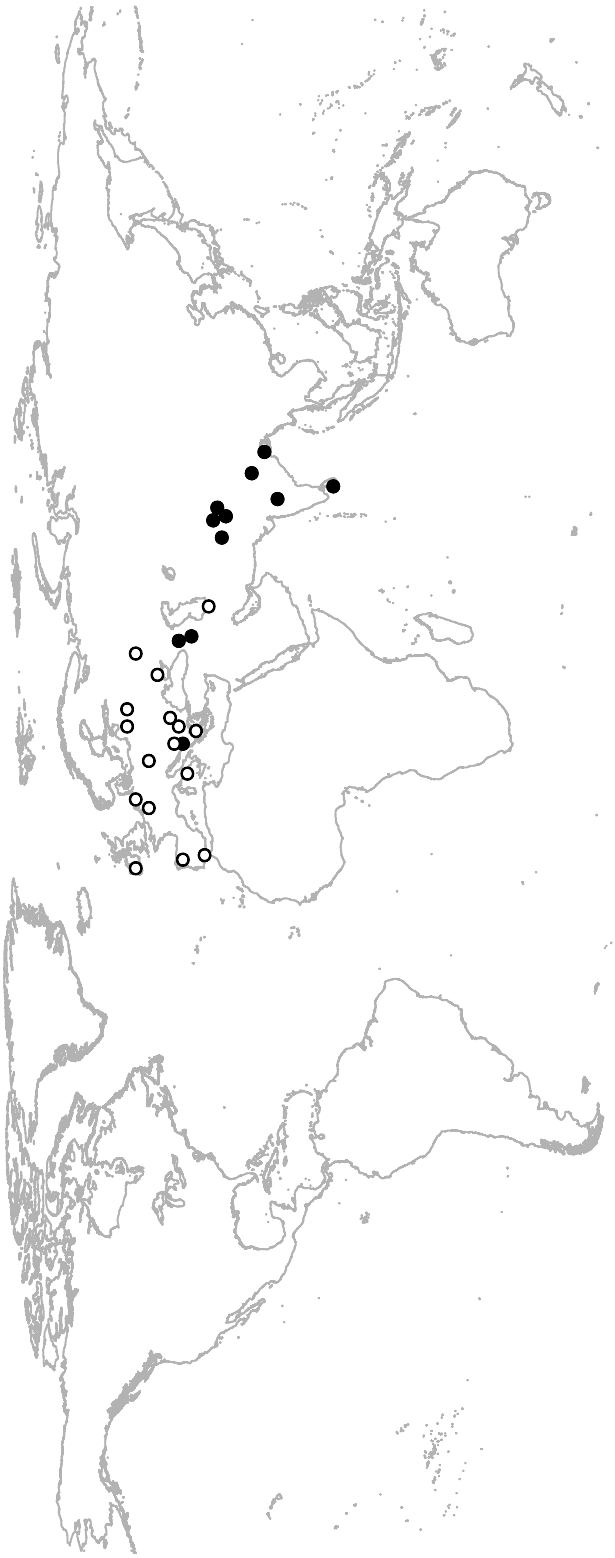
(c) Residence strategy (prevailing mode)

Figure B.2: Map illustrating the geographic distribution of the recoded *EA* data in Table B.2. Colours express the residence strategy (white: neolocal; grey: uxorilocal; black: virilocal), as per Figure 5.4a.



(d) Residence strategy (alternative mode)

Figure B.2: Map illustrating the geographic distribution of the recoded *EA* data in Table B.2. Colours express the residence strategy (white: neolocal; grey: uxorilocal; black: virilocal), as per Figure 5.4b.



(e) Residence strategy (binary)

Figure B.2: Map illustrating the geographic distribution of the recoded *EA* data in Table B.2. Colours express the residence strategy (white: neolocal; black: non-neolocal), as per Figure 6.2b.

Appendix C

BayesMultistate and BayesDiscrete

In this appendix I provide additional information on the phylogenetic comparative method used for the analyses presented in Chapters 4 to 6. I introduce the Bayesian approach to phylogenetic comparative analysis in Section C.1, and the Markov chain Monte Carlo (MCMC) simulation techniques used in this framework in Section C.2; in Section C.3 I provide details on implementation of the method in BayesMultistate and BayesDiscrete. For clarity, the discussion focuses on the simplest case of one binary trait, as in the analysis in Chapter 4; this is easily extended to the case of one ternary trait, as in the analysis in Chapter 5, or to the case of two binary traits, as in the analysis in Chapter 6. The specifics of these cases are detailed in the methods sections of the relevant chapters (Sections 4.2.3, 5.2.3 and 6.2.3). A general introduction to the Bayesian MCMC approach to phylogenetic comparative analysis is in Section 1.2.3.2.

BayesMultistate and BayesDiscrete are available as part of the BayesTraits package (Pagel and Meade n.d.) from `http://www.evolution.rdg.ac.uk/BayesTraits.html`. Unless otherwise specified, the information in this appendix is based on Pagel and Meade (2005, 2006), Pagel et al. (2004), and on the BayesTraits manual (Pagel and Meade n.d.).

C.1 The Bayesian approach

BayesMultistate and BayesDiscrete attempt to discover the evolutionary pathways that resulted in the observed distribution of states for the trait(s) of interest across a sample of taxa. This requires a phylogenetic tree model representing the evolutionary history

of the taxa, and a model of how the trait(s) have evolved on the tree(s). BayesMultistate and BayesDiscrete use a continuous-time Markov model to describe the evolution of the trait(s) along the branches of a tree. Under this model, a discrete trait can switch repeatedly between its possible states in any of the branches of the tree. For example, in the simplest case of one binary trait taking states 0 and 1, the trait can switch repeatedly between its two states, with rate parameters q_{01} and q_{10} measuring the instantaneous rates of change respectively from 0 to 1 and from 1 to 0. The rate parameters are used to define the probabilities of these changes, the character states at internal nodes on the tree, and the likelihood of the data, that is, the probability of the data given the tree and the model of trait evolution specified by the rates (Pagel 1994, 1997, 1999). Four model categories are possible for one binary trait taking states 0 and 1, described by the rate parameters q_{01} and q_{10}: q_{01} and q_{10} may take distinct positive values, they may take the same positive value, or either one may be set to zero while the other takes a positive value. The number of rate parameters increases rapidly with number of states per trait and with number of traits: for example, there are six rate parameters for one ternary trait, and eight rate parameters for two binary traits. Consequently, the number of possible model categories also increases rapidly, with 21,146 possible categories for two binary traits.

The maximum-likelihood implementation of BayesMultistate and BayesDiscrete attempts to find the values of the rate parameters and of ancestral states of the trait(s) at internal nodes on the tree that are most likely to have produced the observed data (Pagel 1994, 1997, 1999). The Bayesian implementation uses the likelihood to estimate the posterior probability of the rate parameters and of ancestral states, that is, their probability given the data and model of trait evolution. The posterior probability of a parameter value is a quantity proportional to the product of its likelihood and prior probability. The prior probability of a parameter value is specified *a priori*, i.e. without reference to the data, to reflect one's belief about the parameter; estimation of the posterior probability amounts to "updating" this belief in light of the information contained in the data, as measured by the likelihood (Lewis 2001). For example, using a uniform prior distribution on the rate parameters means that all values of the rate parameters are believed *a priori* to be equally likely (Section C.3).

Posterior probabilities represent a more intuitive measure of the fit between the data and the model of evolution than likelihood estimates (Huelsenbeck et al. 2002;

Lewis 2001). However, they cannot be computed analytically in a phylogenetic context. For the purpose of phylogenetic comparative analysis, calculation of the posterior probability of a parameter value involves integration over all values of the parameter. Additionally, in order to account for the effect of phylogenetic uncertainty on the posterior probability of the parameter, it involves a summation over all possible tree topologies representing how the taxa are related; in turn, for each of the possible topologies, it involves integration over all possible values of the branch lengths and other parameters in the model of evolution used to infer the tree. Phylogenetic comparative analysis in a Bayesian framework is therefore performed through MCMC simulation, as described in Section C.2. Similarly, phylogenetic tree-building analysis in a Bayesian framework is performed through MCMC simulation (see Felsenstein 2004, Chapter 18 and Yang 2006, Chapter 5): this produces a posterior probability sample of trees, that is, a sample in which trees are present in proportion to their posterior probability; the posterior probability of a tree represents the probability that the tree is correct (Huelsenbeck et al. 2001; Section 4.2.2). Alfaro and Holder (2006) review issues linked to the selection of prior probabilities in this context.

C.2 MCMC methods

Given a posterior probability sample of trees, BayesMultistate and BayesDiscrete estimate the posterior probability distributions of rate parameters and of ancestral states through a Markov chain implementing the model of trait evolution. For one binary trait taking states 0 and 1, the model of evolution is defined by the rate parameters q_{01} and q_{10}, the likelihood function, the prior probability distributions of the rates, and the posterior probability distribution of trees in the tree sample.

Mathematically, a Markov chain is a random process in which the next state depends only on the current state, that is, the next state is independent of where the process was previously (Felsenstein 2004, p. 293). MCMC methods are a class of algorithms for sampling from a probability distribution, based on constructing a Markov chain that has as its stationary distribution the desired distribution (Huelsenbeck et al. 2001); for BayesMultistate and BayesDiscrete, this is the posterior probability distribution of the parameters of interest to the comparative question. Specifically, BayesMultistate and BayesDiscrete use the Metropolis-Hastings algorithm (Hastings 1970; Metropolis et al.

1953) to simulate a random walk across the universe of possible states in the model of trait evolution, and to periodically sample from the states visited. States in the chain correspond to a set of parameters values and a tree drawn from the tree sample. Schematically, starting from a random state, at each step in the chain a tree is drawn at random from the sample of trees, and values are proposed for rate parameters and for ancestral states. Whether a new state is accepted, and thus added to the sample, is determined by comparing the likelihood of the new state to the likelihood of the current state in the chain. States with better likelihood are always accepted, whereas states with worse likelihood are accepted only a proportion of the time equal to the ratio of the likelihood of the new state to the likelihood of the current state; if the new state is rejected, the current state is added to the sample again. Through this process, the chain visits states in proportion to their posterior probability; therefore, if the chain is run for a large number of steps, the distribution of states in the sample produced by the chain closely approximates their posterior probability distribution. Consequently, the proportion of the time that any state appears in the sample is a valid approximation of its posterior probability (Holder and Lewis 2003; Lewis 2001).

A particular implementation of MCMC methods, reversible jump (RJ) MCMC (Green 1995), can be used to additionally estimate the posterior probability distribution of the possible model categories; in this case, at each step in the chain q_{01} and q_{10} are assigned the same positive value, distinct positive values, or either one is set to zero while the other is assigned a positive value. Thus, an RJ-MCMC chain samples simultaneously from the posterior probability distributions of model categories and of the parameters in the model of trait evolution.

Combining estimates over the sample produced by the chain corresponds to "averaging" inferences over uncertainty in the phylogeny, in the parameters of the model of trait evolution, and, in the RJ-MCMC case, in the model itself. Crucially, the validity of the inferences depends on convergence of the chain to its stationary distribution, that is, to the posterior probability distribution of the parameters of interest to the comparative question; in turn, this depends on the ability of the chain to wander through "state space" effectively (Section C.3).

C.3 Implementation

MCMC chains are constructed to ensure that they converge to their stationary distribution. In BayesMultistate and BayesDiscrete, the chain specifications described in this section are determined through a series of preliminary runs, using the programmes in both maximum-likelihood and MCMC mode.

At each step in an MCMC chain BayesMultistate and BayesDiscrete change the values of the rate parameters by an amount specified by the rate deviation parameter, set through the `ratedev` command. The rate deviation parameter is adjusted iteratively to produce an acceptance rate of between 20 and 40% of the proposed changes: at lower rates, the chain may fail to explore state space effectively; at higher rates, the chain would accept nearly all proposed states, such that successive states would be highly correlated. In any case, some degree of auto-correlation between successive states is inevitable; therefore, the chain is "thinned" through the `sample` command, which sets the interval for sampling the states visited by the chain. Wide intervals ensure the near-independence of successive states sampled by the chain.

Because the chain is started from a random state, it will usually take some time to find regions of state space with high posterior probabilities. Convergence of the chain to the posterior probability distribution, that is, to its stationary distribution, is assessed by plotting the $\log_e$(likelihood) values of the sampled states against iteration. In a typical run the $\log_e$(likelihood) values increase steadily and then fluctuate randomly up and down around a stable value. States sampled during the initial climbing phase, known as "burn-in period", are discarded; in BayesMultistate and BayesDiscrete the length of the burn-in is set through the `burnin` command. Whether the chain does reach convergence largely depends on the length of the walk, which is set through the `iterations` command in BayesMultistate and BayesDiscrete. However, the random nature of the process means that it is not possible to know in advance how long it takes for the chain to reach convergence — hence the reference to the Monte Carlo casino in the name of the procedure (Felsenstein 2004, p. 292). Relatedly, the chain may fail to explore state space effectively, producing a sample that does not reflect the posterior probability distribution even after very long runs. For example, a chain may be "stuck" in one region of state space for a large number of iterations after the burn-in phase, failing to visit regions with higher posterior probabilities. Therefore,

a number of separate chains are run, each started from a different random state; if the chains produce comparable samples, they likely converged to the same region in state space, i.e. to their stationary distribution — in this case, it is safe to assume that the distribution of states in the samples approximates the posterior probability distribution.

As noted in Section C.1, the posterior probability of a parameter value is a quantity proportional to its likelihood and prior probability. At present, BayesMultistate and BayesDiscrete implement three prior probability distributions on the rate parameters: uniform, exponential, and gamma. A uniform prior, specified by a range, is used if all values of the rate parameters are believed to be equally likely. An exponential prior, specified by a mean, is used if small values of the rate parameters are believed to be more likely than large ones. A gamma prior, specified by a mean and variance, is used if the distribution of parameter values is believed to be right skewed, with small or small to intermediate values of the rate parameters more likely than large ones. Selection of prior probability distributions represents an issue for concern in the Bayesian approach, because it involves some degree of arbitrariness. One option is to use uniform ("uninformative") priors; unless the signal in the data is particularly strong, however, this strategy may result in the chains not visiting state space effectively. "Informative", i.e. non-uniform, priors are used in this case. Having specified the shape of the prior distribution (exponential or gamma), one can remain agnostic about the values of its parameters (i.e. about the value of the mean for the exponential and of the mean and variance for the gamma), by making BayesMultistate and BayesDiscrete estimate them from the data. This requires specification of a "hyperprior", itself a uniform distribution specified by a range; BayesMultistate and BayesDiscrete draw values at random from the hyperprior and use them to seed the parameters of the desired prior distribution.